

THE FOOD OF THE BROWN TROUT (*SALMO TRUTTA L.*)

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I. INTRODUCTION.

ALTHOUGH many anglers have, from time to time, investigated the contents of the stomachs of trout, their records are seldom published. The data they obtain are for the immediate purpose of discovering the fly upon which the fish are feeding, in order that they may be guided in the selection of a lure with which to fish. Tate Regan (10) states that the diet of trout "consists of shrimps, water-snails, insects, worms, etc., and small fish, such as minnows or the young of their own species," and Southern and Gardiner (12) studied the food of trout in Lough Derg and the Shannon with special reference to the occurrence of planktonic organisms in the stomachs. Books on angling such as those of Halford (2), Moseley (4) and Platts (9) contain scattered references to the results of stomach examinations and, in the *Salmon and Trout Magazine*, Rushton (11) has listed the organisms found in trout but the results are not systematised. Mottram (5) has given an account of the food of trout fry, and Dahl (1), Muttkowski (6) and Phillips (8) have studied the food of river trout in Norway, Yellowstone National Park, U.S.A. and New Zealand respectively. The material here presented is apparently more extensive than has hitherto been examined in this country, and it may therefore be desirable to place the results on record with the object of obtaining a more generalised view of the food of trout.

The data in this paper were obtained during an investigation of the River Itchen in Hampshire by the Ministry of Agriculture and Fisheries and during a survey of the non-tidal section of the River Tees, on the borders of Yorkshire and Durham, undertaken by the Ministry as part of the programme of the Water Pollution Research Board of the Department of Scientific and Industrial Research. The author is indebted to the Ministry and to the Department for permission to publish the results. He also expresses his thanks to Mr A. C. Gardiner, formerly Assistant Naturalist on the staff of the Ministry, under whose direction work on the food of fishes was first begun, and for his permission to use the Itchen material which he had collected and examined.

II. MATERIAL AND METHODS.

In the absence of a commercial fishery for brown trout such as exists for sea trout (7) the collection of material has depended entirely on the good will of anglers, and the author is greatly indebted to those who have collaborated in this work by preserving the stomachs of the fish they have caught and send-

ing them in for examination. By this method 104 stomachs from Tees trout were obtained in the period May, 1929, to August, 1931. The Itchen material consists of 29 stomachs similarly obtained between June and September, 1925. The Tees material was all obtained during the legal fishing season, March 15th to September 30th, so there are no data on the food during winter months.

All the fish were caught by hooks. The usual method of fishing in the Tees is the "wet fly." The bait consists of a series of artificial flies, generally three, which are allowed to sink in the stream and are supposed to imitate the nymphal stages of Ephemeroptera and Plecoptera. Occasionally a worm is used as bait. The Itchen material was all obtained by fishing with a "dry fly," a single artificial fly floating on the surface of the water and imitating the winged insect. This method of catching fish for the purpose of investigating their food is open to the objection that the fish are attracted to the surface to feed and therefore the catches are weighted by an excess of surface feeding while bottom feeders are not sufficiently represented. It may be pointed out, without denying that the criticism may have some weight, that the proportion of bottom-feeding fishes taken on the Itchen with a floating fly was greater than on the Tees with a sunken fly.

Phillips (8) states that when a fish is hooked it frequently vomits the food in the front part of the stomach. Although this habit has not been observed it probably occurs, since many fish contained nothing in the front part while the hind part was full.

The contents of the stomachs consisted almost entirely of animal matter, and the identification of organisms was dependent on the degree of digestion they had undergone. In general, while food in the front limb of the U-shaped stomach was almost undigested and therefore comparatively easy to identify, that in the hind limb was somewhat more digested and therefore more difficult and the identification of food in the intestine was purely a matter of luck. Indigestible matter such as snail shells and caddis cases is of course recognisable, and certain organisms, for example *Gammarus pulex* and *Ephemerella* sp. nymphs, are digested into characteristically coloured masses, the former yellow and the latter dark crimson, but beyond these it is usually impossible to identify material in the intestine. In a preliminary study such as this no attempt was made to carry identification to species. There are very few cases in which the larvae of Diptera, Trichoptera, Ephemeroptera, and Plecoptera, can, even when fresh, be referred to their species, as their life histories have not yet been worked out. The identification of adults of these orders depends largely on an examination of genitalia, and as in the stomachs the flies were represented often only by heads or legs and wings, the softer abdomen being digested, again specific identification was not obtained. In general in compiling the results the insects have been classified into large groups, partly on account of the identification problem mentioned above, and partly also because the numbers dealt with are comparatively small and it would seem better to treat the material in as broad a manner as possible than to attain indefiniteness by

insisting on specific differences. It is clear therefore that the results here presented will give no answer to the question whether a trout prefers one species, or even one genus, of, say, caddis flies, to another, but it is hoped that the nature of the food of trout will be made clear. Full notes which were made when the stomachs were examined are, however, available for inspection by any one interested upon application to the Ministry.

III. THE RESULTS OF STOMACH EXAMINATIONS.

The trout is almost entirely carnivorous. In only two cases was vegetable matter found in the stomach. In one there was a quantity of bread and in another a grass seed, but no remains of water plants were found. A list of the commoner organisms found in the stomachs of fish from the Tees and Itchen is given in Tables I and II respectively.

Table I. *The food of Tees trout*
(weight 4 oz.-1 lb.).

Number examined 104.

| Food material | Percentage of total stomachs in which found |
|---|---|
| Pisces | 5.8 |
| Diptera | |
| Adult | 28.8 |
| Chironomid larvae | 23.1 |
| <i>Simulium</i> larvae | 6.7 |
| Coleoptera | |
| Land forms | 14.4 |
| Water forms | 7.7 |
| Hemiptera | |
| Aphidae | 6.7 |
| Trichoptera | |
| Adults | 26.9 |
| Free-living larvae | 29.8 |
| Cased larvae | 26.0 |
| Ephemeroptera | |
| Adult Heptageniidae | 11.5 |
| Larval Heptageniidae | 23.1 |
| Adult Baetinae | 16.3 |
| Larval Baetinae | 22.1 |
| Plecoptera | |
| <i>Perla</i> and <i>Perlodes</i> adults | 4.8 |
| <i>Perla</i> and <i>Perlodes</i> larvae | 7.7 |
| Adult Leuctridae | 3.8 |
| Larval Leuctridae | 3.8 |
| Crustacea | |
| <i>Gammarus pulex</i> L. | 7.7 |
| Mollusca | 2.9 |
| Oligochaeta | 2.9 |
| Others | 21.2 |
| Empty | 2.9 |

Table II. *The food of Itchen trout*
(weight 1-2 lb.).

Number examined 29.

| Food material | Percentage of total stomachs in which found |
|-------------------------------------|---|
| Diptera | |
| Adults | 17.2 |
| Hymenoptera | |
| Adults | 10.3 |
| Coleoptera | |
| Land forms | 10.3 |
| Hemiptera | |
| <i>Corixa</i> sp. | 27.6 |
| Trichoptera | |
| Adults | 27.6 |
| Cased larvae | 34.5 |
| Ephemeroptera | |
| <i>Ephemerella</i> sp. larvae | 24.1 |
| <i>Ephemerella</i> sp. adults | 10.3 |
| <i>Ephemerella</i> sp. larvae | 13.8 |
| <i>Baetis</i> sp. adults | 13.8 |
| <i>Baetis</i> sp. larvae | 20.7 |
| Unidentified nymphs | 10.3 |
| Crustacea | |
| <i>Astacus pallipes</i> Lereboullet | 27.6 |
| <i>Gammarus pulex</i> L. | 37.9 |
| Mollusca | |
| <i>Valvata piscinalis</i> (O.F.M.) | 13.8 |
| Other Mollusca | 24.1 |
| Others | 24.1 |
| Empty | 6.9 |

Notes on Tables I and II. The fishes recorded in Table I were minnows (*Phoxinus laevis* Agass), bullheads (*Gobio gobio* L.) and in one case cyprinoids, probably dace (*Leuciscus leuciscus* L.).

No attempt was made to name adult Diptera. They consisted very largely of *Simulium* of various species, Culicids and Chironomids. In three stomachs from the Itchen there were present bluebottles (*Calliphora* sp.).

The Hymenoptera in Table II consisted of ichneumons, wasps and ants. Upon occasion ants and bees were found in the Tees stomachs and are included in the class "Others."

The Coleoptera were separated only into terrestrial forms such as weevils, cockchafers, etc., and aquatic forms.

The adult Trichoptera of the Tees samples consisted largely of *Leptocerus* spp., though *Brachycentrus subnubilus* Curt. (the grannom) and *Agapetus comatus* Pict. were also recorded. The Itchen caddis consisted largely of *Odontocerum albicorne* Scop. with occasional specimens of *Silo* sp. The larvae have been divided into those which do not make a regular movable case, including such forms as *Hydropsyche* sp., *Rhyacophila* sp., *Agapetus* sp. and *Polycentropus* sp. and those which do. In the Itchen samples only one, a *Rhyacophila* sp., was recorded and is therefore classed with "Others," but in the Tees material these larvae were very abundant, *Hydropsyche* sp. making up the bulk of them. The cased forms of the Tees consisted largely of *Leptocerus* spp.; *Brachycentrus* sp. and an unidentified Limnophilid were also recorded. In the Itchen the commonest cased caddis larva was *Odontocerum albicorne*.

The Heptageniidae recorded from the Tees include the genera *Rhithrogena* and *Ecdyonurus*. The Baetinae include *Baetis* and *Ephemerella*.

The Mollusca recorded from the Tees consist of *Limnaea peregrina* O.F.M. and *Ancylus fluviatilis* O.F.M. The same two genera are included among "Other Mollusca" in Table II together with *Planorbis* sp., *Bythinia tentaculata* Linn., *Pisidium* sp. and *Sphaerium corneum* (Linn.).

The Oligochaeta include Lumbricids in two cases and Tubificids in one. Among "Others" of the Tees samples are *Eristalis* larvae, Tipulid larvae, millipedes, *Calliphora* larvae, *Sialis* larvae, *Gerris* sp., leeches and black slugs. The Itchen "Others" include *Gerris* sp., *Notonecta* sp., Coleopterous larvae, leeches and *Asellus aquaticus* L.

The number of species and of individuals found in one stomach varies enormously. Where the food is large, as for example fish, crayfish or *Perla* larvae, then the numbers are naturally small. A few fill up the stomach and there is no room for other species, but where small animals such as *Simulium* and *Baetis* sp. are being taken, then the individuals may be numerous and the number of species large, though it generally happens that the bulk of the food consists of one species only. One Tees stomach contained 250 *Simulium* sp., though such quantities are rare. As an example of the catholic nature of a trout's taste the contents of a stomach taken in August, 1930, from the Tees may be given in full: *Simulium* sp. 10, *Simulium* sp. larvae few, Chironomid larvae very numerous, bee 1, caterpillar 1, caddis fly 1, *Leuctra* sp. 10, *Leuctra* sp. larvae very numerous, *Baetis* sp. larvae very numerous, black slugs 4,

Lumbricids 4, Tubificids 1. For comparison a more typical example, from the Tees in June, 1931, is: Chironomid larvae 2, *Ecdyonurus* sp. larvae 1, *Ephemerella* sp. larvae 4, *Baetis* sp. larvae 4, *Ancylus fluviatilis* 1.

Discussion. It is clear from Tables I and II that practically anything that comes near is a possible food for trout, but, for the purpose of this paper, it will be sufficient to consider only the commonest, and the distribution of air-borne and water-borne foods. It will be seen from Table III that the commonest foods of the two rivers when compared are strikingly similar in some cases and equally dissimilar in others.

Table III.

| River Tees | | River Itchen | |
|-------------------------------------|---|-------------------------------|---|
| Food material | Percentage of total stomachs in which found | Food material | Percentage of total stomachs in which found |
| 1. Free-living Trichopterous larvae | 20·8 | 1. <i>Gammarus pulex</i> | 37·9 |
| 2. Adult Diptera | 28·8 | 2. Cased Trichopterous larvae | 34·5 |
| 3. Adult Trichoptera | 26·9 | 3. Adult Trichoptera | 27·6 |
| 4. Cased Trichopterous larvae | 26·0 | 4. <i>Corixa</i> sp. | 27·6 |
| 5. Chironomid larvae | 23·1 | 5. <i>Astacus fluviatilis</i> | 27·6 |
| 6. Heptageniid larvae | 23·1 | 6. <i>Ephemera</i> sp. larvae | 24·1 |
| 7. Larval Baetinae | 22·1 | 7. Other Mollusca | 24·1 |
| | | 8. <i>Baetis</i> sp. larvae | 20·7 |

Thus adult Trichoptera and cased Trichopterous larvae are very nearly equally abundant, while with the exception of *Baetis* larvae the others are very different. Free-living caddis larvae which head the list in the Tees have only occurred once in the Itchen. Adult Diptera are very common food in the Tees but only moderately so in the Itchen. Chironomid and Heptageniid larvae were common in the Tees samples but were not recorded from the Itchen. On the other hand *Gammarus*, which occupies first place in the Itchen foods, is comparatively rare in the Tees samples, and *Corixa*, *Astacus* and *Ephemera* larvae are unrepresented in the Tees stomachs.

It is axiomatic that the food of trout is dependent on the available supply and is limited to those organisms which live or are drowned in the stream or come on to its surface. The differences and similarities of Table III can probably be completely explained by the difference of the fauna of the two rivers. A short account of the fauna of the Itchen has been published (3), and an account of the fauna of the Tees will be included in a Water Pollution Research Technical Paper of the Department of Scientific and Industrial Research on the biological and chemical survey of the River Tees to be published later. It is unnecessary to give here a full account of the fauna of these rivers, and only such features as bear directly on the problem will be considered. Free-living Trichopterous larvae, especially *Hydropsyche* sp., are very common in the lower reaches of

the Tees and scarce in the Itchen, and as they do not appear to be distasteful to the trout their greater abundance in the Tees stomachs is merely a reflection of their occurrence in the rivers. The same applies to Diptera and Heptageniid larvae. *Gammarus pulex* is very abundant in the Itchen and comparatively rare in the Tees. *Corixa* sp., *Ephemera* sp. larvae and *Astacus* are common in the Itchen and very rare in the Tees. It seems clear, however, that no common species is much more valuable as a trout food than any other. The percentage of common foods are so even, and correspond so closely with the relative abundance of the organisms in the river that it can only be assumed that the trout feed indiscriminately on the most readily available food. There is, however, one striking feature. The Plecoptera *Chloroperla grammatica* Scop. and its allies *Isopteryx torrentium* Pict. and *I. tripunctata* Scop. are very common as larvae in the Tees in spring and as adults on the water surface in summer, and yet they have not been found in the stomachs examined. This is confirmed by Halford (quoted in Mosely, 4) and seems to indicate that these forms are not eaten by trout.

Surface and sub-surface food. A broad classification of the food can be made according to its origin, whether it is found on the surface of the water or whether it is found in the water. In Table IV there are given the number and percentage of stomachs containing surface, sub-surface and a mixture of the two.

Table IV. *The food of trout. Tees and Itchen compared.*

| | River Tees | | River Itchen | |
|------------------------------------|------------|-------|--------------|-------|
| | | % | | % |
| Surface food only | 19 | 18.2 | 1 | 3.4 |
| Mixed surface and sub-surface food | 55 | 52.9 | 16 | 55.2 |
| Sub-surface food only | 27 | 26.0 | 10 | 34.5 |
| Empty | 3 | 2.9 | 2 | 6.9 |
| Total | 104 | 100.0 | 29 | 100.0 |

It will be seen that in each river the majority has been feeding on a mixture of the two, showing that the fish do not at one time feed exclusively on surface, and at another time on sub-surface organisms.

In spite of the fact that the Itchen trout were all caught by a floating fly the percentage of stomachs which contained only surface food is much lower than in the Tees. This can be explained again by the differences in the fauna of the two rivers. The Itchen has a large permanent water population consisting of Crustacea. The fauna of the Tees is composed mainly of insect larvae, and naturally as these become adult and leave the water, the fauna becomes impoverished and the trout are forced to seek their food on the surface. In Table V the seasonal occurrence of food of different origin is given, and it shows that in August, when most insects have left the water and the eggs they produce have not yet hatched, 50 per cent. of the stomachs contained only surface food.

Table V.

Figures show numbers of stomachs.

| | April | May | June | July | August | September |
|-------------------------------|-------|-----|------|------|--------|-----------|
| Surface food only | 0 | 1 | 1 | 5 | 11 | 1 |
| Mixed surface and sub-surface | 10 | 7 | 15 | 11 | 8 | 4 |
| Sub-surface food only | 6 | 0 | 12 | 1 | 3 | 5 |

The greater part of the surface food as shown in Tables I and II consists of aquatic Diptera, Trichoptera, Ephemeroptera and Plecoptera. These insects after leaving the water have to return to it to lay their eggs, and it is therefore natural that they will make up the greater part of the surface food. That other insects are taken equally well is also shown by the tables, though the chance of their finding their way to the river will not be so great. It is significant that weevils and other tree-living beetles and aphids are the most abundant land insects, and it is clear that they fall from trees overhanging the river, and also that such trees will be a material help to the food supply of trout. In New Zealand Phillips (8) has obtained similar results. The occurrence of other insects on the water surface, such as Hymenoptera, Calliphora, etc., is purely a matter of chance, and except that they are eaten by trout when occasion offers there is no likelihood that they are an important source of food.

IV. SUMMARY.

1. The food of brown trout (*Salmo trutta* L.) living in rivers has been investigated by the examination of the stomach contents of 133 fish, 104 from the Tees and 29 from the Itchen.
2. The trout is carnivorous and eats almost any animal of a suitable size that presents itself, either in the water or on its surface.
3. The commonest foods, whether surface or sub-surface, are those which are commonest in or on the stream at the time the trout is feeding.
4. The differences in stomach contents of fish from the rivers can probably be completely explained by the differences in the fauna.
5. There is no evidence of specially attractive foods, but it is suggested that Plecoptera of family Chloroperlidae are not eaten by trout.

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THE FORECASTING OF THE EAST ANGLIAN HERRING FISHERY

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(*With four Figures in the Text.*)

I. INTRODUCTION.

ONE of the most interesting and important branches of marine biology is the study of the life history of the herring. It has formed the subject of research for many years, from the early days when it was discovered that the scales of fishes carried certain markings on them which gave the clue to their age. The initiation of the investigations into the composition of commercial shoals of herrings was undoubtedly the work of certain Norwegian fishery experts, and one cannot mention even the most elementary work in this research without being extremely grateful to Prof. Hjort of Oslo University, as director, Mr Knut Dahl, and especially Mr Einar Lea.

In his preliminary studies on the herring, Mr Lea investigated thoroughly the scale covering of the fish, showed beyond all doubt that the rings on the scale were annual, and also that there was an almost linear relationship between the growth of the scale and the growth of the fish. These several points having been established, the task of beginning the work in the southern North Sea was comparatively simple. It only remained to be demonstrated that the herrings of this area exhibited the same characteristics in their scales as those from Norwegian waters.

Accordingly, the first work of this department was to examine samples of fish from the southern North Sea on the lines laid down by Einar Lea, and, had the results of the examination not justified the adoption of his methods, it would have been necessary to alter or modify them to suit our material. Fortunately, this was unnecessary, for the first two or three years showed that we were arriving at results similar to those obtained in Norway.

II. HERRING FISHERIES AND SHOALS.

The fishery with which we are immediately concerned is that which is exploited by the drifter fishermen along the coastal waters of England from Northumberland to the Straits of Dover. The outer limit of this drift-net fishery is about 30 miles from the shore, so the area fished may be taken as a strip of this breadth down the whole extent of the coast.

The drifters, as their name implies, are small vessels which remain almost stationary with regard to the body of water in which they are working. To them is attached the fleet of about 90 nets which stretch away through $2\frac{1}{2}$ miles of

sea and their movement in space is controlled by the tidal current and wind. Unlike the trawl, the nets catch the herrings as they swim through the water, so the amount of fish caught depends on the concentration of the herrings rather than on the area of ground covered. It thus becomes obvious that for a successful fishery the times of fishing must coincide with the periods during which the herrings are gathered together in dense shoals, and this they do for two important reasons, (a) for feeding, (b) for spawning.

In the southern North Sea, most of the spawning takes place between September and January, and the grounds where the eggs are deposited lie mainly west of long. 3° E. The spawning begins in late August or September to the north of the Northumberland coast, in the vicinity of the Longstone lighthouse. A little later, a slightly greater spawning occurs off the Yorkshire coast, in the neighbourhood of Whitby; and in October and November the maximum of the autumn spawning is reached on grounds between the Yorkshire coast and the Dogger Bank. In October also, spawning fish are found opposite the entrance to the Wash, but after that time there comes a lull, and it is not until December that the next spawning is noticed much further south at the entrance to the Straits of Dover. What is probably the greatest spawning ground of all has been found to be that on the north French coast between Boulogne and the mouth of the Seine. It is here that the great shoals of herrings which appear off East Anglia each autumn, congregate to deposit their eggs—actually outside of the North Sea. The reason for this migration becomes clearer when we consider the nature of the egg and the peculiarities of the current system of the area. The herring is one of the few fish which lay their eggs actually on the sea floor. Here the eggs lie in large gelatinous masses where they are fertilised at the time they are deposited. On hatching out, the larval herring becomes at once dependent on the movements of the water in which it lives, since at this stage it is unable to swim against a stream. The normal flow of water through the Dover Straits is from the Channel to the North Sea, which means that the larvae of herrings which have spawned in the eastern part of the Channel will be carried back into the North Sea and so replenish the stock which has been depleted by mortality, either through natural death or the action of man. Thus, in this respect, the herring is similar to the salmon in that it goes up-stream to spawn.

The fisheries based on feeding shoals are less important than those which rely on spawning fish. At present the chief one is that which occurs annually off the Northumberland coast in June. The area at this time is particularly rich in planktonic forms¹ which constitute the main diet of the herrings, and the feeding fish are almost entirely young herrings—many of them immature and in their third year. There are indications of another feeding ground further south in the neighbourhood of Yarmouth in June, but although we know that feeding herrings are to be found there, the location of the actual concentration

¹ *Calanus*, *Temora*, some Schizopods and often young sand-eels.

of food has not definitely been established. The fish which are found here are larger and older than those which are caught off the Northumberland coast, and there is evidence to show that these larger fish are probably the same as those which appeared in the spawning concentrations in the previous autumn.

III. AGE DISTRIBUTION.

Now, a word as to the age composition of these various shoals which appear along the coast. It has been found that with the exception of the Northumberland feeding shoals which are mainly composed of three-year-old fish, the bulk of the herrings which are caught from Northumberland to the north Norfolk coast in the autumn, are in their fourth year, and it is usual to find that 30-50 per cent. of the catches are composed of this age-group. As this happens every year, it is obvious that these grounds receive the new-comers to the stock, and that after they have spent one season in these waters they join another shoal composed mainly of larger and older fish. This brings us to the chief fishery of the southern North Sea—that which takes place off the East Anglian coast in the late autumn from October to December. The concentration here is the greatest known, and the quantities of fish caught are reckoned in millions of hundredweights compared with tens of thousands further north.

It is with these important shoals that we are dealing so far as forecasting is concerned.

This fishery can be divided into two main parts, an early fishing in October and a later fishing in November and December, and it is a regular feature of the area that in the early part the catches are made up mainly of four-year-old fish—as in the northern grounds—while the later fishery depends to a great extent on the older fish from five to ten or eleven years of age.

It has been said above that after four years of age the herrings then join a shoal of older fish. It is with this transference that the present special study deals.

In a fish population, as in a human population, there are two processes going on continually. Firstly, we have the appearance of the newly born individuals, and secondly, the disappearance of the old ones by death, and the survival of the race depends on the rate of immigration being greater than the rate of mortality. The human and fish populations cannot, however, be very closely compared, for, in the former, all individuals, mature and immature, live together in the same community, while in the case of herrings the individuals live in communities which seem to depend on the state of development of the gonads. For instance, as soon as the herrings are sufficiently developed to become more or less free-swimming, they seek the coastal waters where they remain until they are approximately a year old, and it may be that in these in-shore places they can live under conditions which are beneficial to their development. After the first year they then move off-shore to the deeper waters in the central part of the North Sea, and on the eastern and southern slopes of

the Dogger Bank herrings in their second year can be caught in large numbers. It is in the third year that the gonads first show signs of development, and it is therefore at this period of their life that they first make their appearance in the spawning shoals. But all the herrings do not mature at the same time. Only a few of a year-class have their gonads developed at three years of age; the majority are mature at four years, and the remainder at five years. Thus it will be seen that the immigration into the spawning shoals takes place in three stages occupying the period when the year-class is growing from three to five years of age.

After five years it may fairly be assumed that practically all the herrings have become spawners, and it is now that we have to deal solely with mortality, and so far as the fishery is concerned, it matters little whether this mortality is caused through natural causes or by the act of man and his fishing implements. Before proceeding, it must be remembered that these remarks apply only to the herrings of the southern North Sea, for in other areas it has been found that the age of first maturity may be quite different. In Norwegian waters the fish mature at a much greater age than those we are now discussing, while in the Baltic Sea the fish are ripe at a very early age. These changes are accompanied by a much slower mortality rate on the one hand and a quicker rate on the other.

IV. CHANGES IN THE HERRING POPULATION.

We can now review the changes which take place in the main stock of herrings in the southern North Sea from year to year since our investigations began. Each season many thousands of fish are examined for age and length in the shoals which congregate off Norfolk and Suffolk in the autumn for the purpose of spawning in the near future, and in the diagram (Fig. 1) will be seen the age composition of the shoals each year from 1923 to 1931. It was stated earlier that there were two components in this fishery, the young fish which appear in October, and the older fish which arrive in November. It is thus self-evident that great care has to be exercised in the sampling of the stock if even approximately accurate results are to be obtained, for by taking more samples in October than in the later part of the fishery, the total age composition will contain more young fish than would have been the case had the distribution of the samples been reversed.

Our aim is to show the proportion of young fish to old fish in as accurate a manner as possible so that the study of the rate of decrease of each year-class may be carried out with a fair degree of certainty. It was not until 1930 that we were in a position to carry out the sampling in a really satisfactory way, ridding ourselves of the bias which had appeared in the sampling of the earlier years, so, in examining Fig. 1 it must be remembered that the age distribution during the years 1923-9 is more of a qualitative nature than quantitative.

Nevertheless, it is possible, even with these figures to obtain approximate results, and, the sampling errors having been eliminated, the results will become more and more accurate with each subsequent year of work.

To return to Fig. 1. It will be seen that the ages of the fish fall between the limits of two to eleven, and also that the numbers at these limits are very small indeed, because the numbers of fish which mature at two years of age are insignificant, as are the numbers of herrings which live, in this area, to a greater age than ten. The effective life of these herrings may be taken as eight years, from the ages of three to ten. It is also to be noticed that the numerical strength of the age-classes varies considerably; that certain age-groups are smaller than the one which is a year older. This means that there must be a great degree of variability in the sizes of the incoming year-classes, for, if the classes were all of the same size a diagram like the one given would be impossible as no year-class could then be smaller numerically in any year than one which is older, since we cannot assume a different rate of mortality for each *year-class*.

Another feature of the figure is the more or less constant shape of the right-hand side of each histogram. This suggests that the East Anglian stock is practically self-contained, and that there is neither much emigration from it, nor any appreciable addition of older fish to it from outside sources. By following each of the year-classes through the diagram, it is apparent that each one increases in numerical value up to the age of four or five years, after

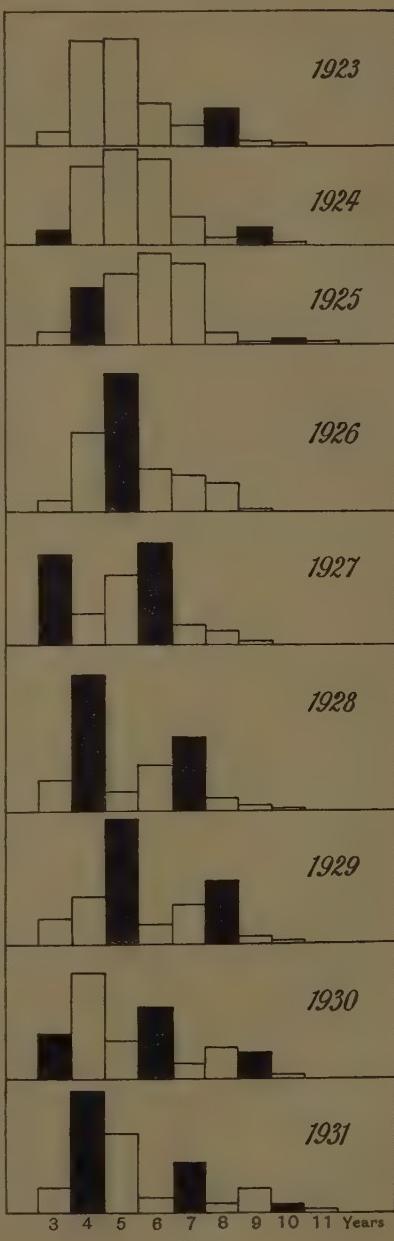


Fig. 1.

which age there is a decrease in numbers, and it is from this point that mortality rates must be calculated.

The most comprehensive work yet published on the mortality of fish populations is that of Einar Lea on the herring stock of the Norwegian coast, and as our own southern North Sea stock is similar in many respects to that of Norway, his methods can usefully be applied in this case.

To understand fully the changes which are taking place it is necessary to know two important factors. Firstly, the rate of decrease from one age to the next—five to six, six to seven, etc., and secondly the average rate of decrease over the whole period from five to eleven years of age.

These can be calculated as follows. Let a, b, c, \dots, n represent the various years of observation, and $a_5, b_5, c_5, \dots, n_5$ all the individuals of five years of age in these years, then the following expression will give that rate of mortality for the interval between the fifth and sixth years:

$$100 \left[1 - \frac{(b_6 + c_6 + d_6 + \dots + n_6)}{(a_5 + b_5 + c_5 + \dots + m_5)} \right].$$

This will be the percentage rate of decrease, and the rates for all the intervals can thus be worked out. The average rate is calculated as follows:

$$100 \left[1 - \frac{(b_6 + c_6 + d_6 + \dots + n_6) + (b_7 + c_7 + d_7 + \dots + n_7) + \dots + (b_{11} + c_{11} + \dots + n_{11})}{(a_5 - b_5 - c_5 - \dots - m_5) + (a_6 - b_6 - c_6 - \dots - m_6) + \dots + (a_{11} - b_{11} - c_{11} - \dots - m_{11})} \right].$$

Without going into the arithmetical work of the above calculations the rates for the East Anglian herrings can be given thus:

The average percentage rate is 36.9 per cent., and the rates for each interval are:

Five to six 27.9 per cent. Eight to nine 56.4 per cent.

Six to seven 32.1 " 63.8 "

Seven to eight 42.7 " 69.6 "

Armed with these factors, it is now possible to calculate the strength of the stock of old fish (i.e. over five years of age) in any year n , if the numbers of each year-class are known for the year $n-1$, but we have also to consider the immigration of the young herrings to the shoal before the final picture is complete.

Here we are dealing with immigrants from the unknown, for until the young three-year-old fish appear in the catches we have no means of defining their numerical strength. Even at the age of three they can only be assessed very approximately, for they are so small that many of them will escape through the meshes of the net with the result that their numbers in the catches are under-estimated.

A rough estimate of the rate at which the young fish increase in numbers from three to five years of age can, however, be obtained in the following way. We can produce a diagram showing the average age distribution of the catches for the whole period under review, from 1923 to 1931, and from the curve, calculate the rate at which the age-classes increase during their earlier years.

Fig. 2 shows the curve which represents the average age of the landings from 1923 to 1931.

From this figure the calculated rate of increase from three to four years of age is 290 per cent. and from four to five years of age there is a slight decrease of 4·3 per cent. The reason that the four and five-year-old fish appear in approximately equal numbers is that the rates of increase and decrease between four and five have just balanced each other, and naturally, the sudden fall in the curve after five years is due to the absence of immigration and the increasing effect of mortality.

Before we can use these figures in a really effective way, the age composition of the catch must be known and the proportion of the young fish to the old should be ascertained in the most efficient manner possible. This at first pre-

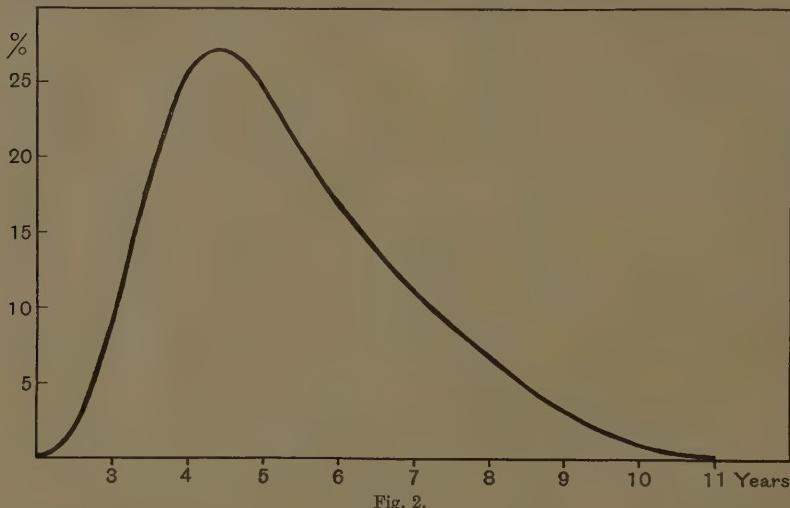


Fig. 2.

sented some little difficulty, because of the patchiness of the herrings on the grounds and the consequent differences in the landings of individual drifters. It was found that on any one day, some vessels would be landing all small fish, some all large, and others a mixture of the two kinds, thus the practice of using samples from fishing vessels would not give a true picture of the landings during the whole season. It was found best to attempt to treat the fishery as a whole and for the purpose of the statistical treatment, to deal only with the herrings on the market and not on the individual ships, and as the fishery is based on two ports, Yarmouth and Lowestoft, it was necessary to carry out the work at each of these places.

Two assistants were employed in the markets during the whole of the season from late September to December, and their duty was to measure all the herrings they could each day, then at the end of each week, the percentage length

composition of the catches at each port was calculated. At the end of the season we then had the complete history of the changes in the landings from week to week, but only as far as the length of the fish was concerned. Concurrently with these observations, four samples of fish—two from each port—were examined at the laboratory, and from these the age distribution in each centimetre length was found. It was now only necessary to apply these distributions to the length groups in the weekly measurements from the markets, in this manner: Suppose that there were 2500 fish whose length was 23 cm., and in the laboratory samples there were 150 herrings of 23 cm. in length whose ages were found to be as follows:

$$\frac{3}{34} \quad \frac{4}{76} \quad \frac{5}{40} \text{ years,}$$

then if the above 2500 fish were divided in the same proportions the resulting figures would give us the numbers of fish at three, four and five years of age respectively. This was done for each centimetre length at each port for every week, and at the same time the quantity of herrings landed during each of these periods was noted, and to obtain the final age distribution for the whole season the figures for each week had to be proportionated according to the variation in the size of the landings. By this means the age-classes were seen in the approximately true relationship which they bore to each other.

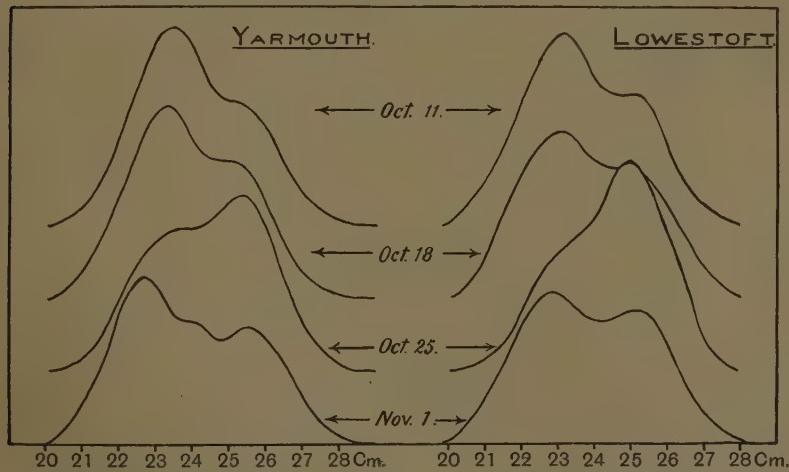


Fig. 3.

This work had not long been in progress when the usefulness of having to duplicate the observations at the two ports became apparent, for the data collected at Yarmouth could be used as a check on those obtained from Lowestoft, and the similarity between the measurements supplied by two men

working independently in two separate markets, showed that the sampling of the stock had been extraordinarily successful. Indeed, such accuracy was not anticipated when the work began.

Above, in Fig. 3, are the measurements at Lowestoft and Yarmouth during the first weeks of the season 1930 in the form of percentage frequency curves. Their similarity is such that any small change in the shoals at Yarmouth is reflected in the landings at Lowestoft, which shows the accuracy of the sampling, since the fleets of both ports were fishing the same stock.

V. FORECASTING.

Now let us turn to the total age composition of the landings for the year 1930, and, using the mortality rates already found, try to calculate the expected age composition of the catch in the year 1931.

The percentage age composition in 1930 was as follows:

| 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | years. |
|-----|------|------|------|------|-----|-----|-----|-----|-----|--------|
| 0·1 | 13·1 | 31·9 | 10·3 | 21·8 | 4·4 | 9·1 | 8·0 | 0·9 | 0·3 | |

The two-year-old fish will be ignored in these calculations for reasons which have already been stated, but the rates of increase and decrease can be applied to the remainder of the age-classes with the following results:

| 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | years. |
|------|------|-----|------|-----|-----|-----|-----|--------|
| 37·9 | 30·5 | 7·4 | 14·8 | 2·5 | 4·0 | 2·9 | 0·3 | |

These figures are not percentages, but only represent the proportions in which the various age classes should be present in the catches of 1931, and they should serve as a guide in attempting to forecast the fishery.

It is seen that the greater part of the fish which are expected on the grounds falls in the age-groups four and five, and the only predominant older group is that of seven years, so from what has already been learned from previous experience, we may expect the October fishing (dependent mainly on young herrings) to be more productive than the later part of the season when the older fish appear. Great care must be exercised in attempting at present to estimate the expected numbers of three-year-old fish from the known number of two-year-olds in the previous year, because the factor is bound to be so great that the most minute error in the estimation of the strength of the two-year-old group in any year will be magnified enormously in the calculation of the three group of the following year.

There is, however, a way of making a rough idea of the strength of the incoming three group. It will be remembered that the summer fishery at North Shields was stated to be dependent mainly on three-year-old fish which appear on the grounds for the purpose of feeding. Now, by observing the fluctuations in the *amount* of this year-group landed in the summer months from the Northumberland grounds from year to year we should be able to arrive at a solution to the fluctuations of the same year-group in the East Anglian

shoals in the following autumn, especially as it has been found that there is a similarity between the fluctuations of these two fisheries as a whole. But, beyond being able to say that there will be a great many three-year-old herrings, or, on the other hand very few in the main autumn shoals, there is at present no justification for relying too much on them in our forecasts.

Having demonstrated the manner in which these forecasts can be made, let us consider the season 1931, with regard to the herring landings from the autumn fishery.

For the purpose of the forecast which was published in a trade journal on August 22nd, 1931, the data collected during the years 1923–30 were used to calculate the rates of mortality. (In the example given to illustrate the method, the whole data up to 1931 were used.) Here in this case the calculated increase from two to three was found by multiplying the strength of the two group in 1930 by 90—this factor being obtained from the average frequency curve for the age distribution in the East Anglian stock—but as we have already seen, this may not be very accurate. The expected proportions of the age-groups in 1931 became as follows:

| 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | years. |
|-----|------|------|-----|------|-----|-----|-----|--------|
| 9·0 | 35·3 | 32·5 | 7·6 | 14·2 | 2·5 | 3·6 | 2·1 | |

Below, in Fig. 4, is shown the expected result and the actual result for comparison. The actual result is shown as a percentage histogram, while the other merely shows the relative strengths of the groups.

The proportions of the older groups—five and over—are similar in the two diagrams, but there were actually more four-year-old fish in the shoals than had been expected by calculation. Nevertheless, the predominance of the four group over the five group was shown.

These forecasts can only give the prospects of the stock of fish in the East Anglian fishery and do not represent the amount of fish which will be taken by the drifters, for in some years gales may upset all calculations. For instance, in November, 1929, a terrific gale caused some £300,000 worth of damage to the fishing fleet, with the result that most of the Scottish boats had to return home long before the season was finished, thus causing the landings of that year to be much smaller than they would normally have been. Again, there are many features of the fishery with which we are not yet acquainted. Why do the herrings appear early one year and later another? It may be that when there is a large quantity of young fish in the shoals there is an early fishing, and if these fish are but poorly represented, then the fishing will be late. But we are not yet sure. We must also study the movements of organisms which are

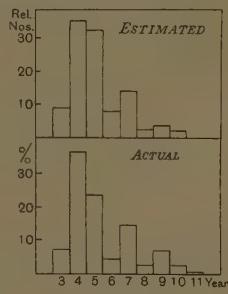


Fig. 4.

definitely distasteful to the herrings—such as *Phaeocystis*, a colonial flagellate of gelatinous nature and which is known to the fishermen as “baccy juice.” They refer to such contaminated water as “stinking” or “weedy” and they have learned to associate such water with poor herring catches.

The appearance of *Phaeocystis* and the like in large masses may have the effect of driving the fish off shore or in some cases on shore according to the location of the concentration, and even a small migration on the part of the herrings may upset all calculations as to abundance, for the grounds usually fished are comparatively small in extent.

Apart from the attempts to estimate the age of the shoals in the southwest of the North Sea, considerable success has been achieved in forecasting the size of the fish, which is of primary importance to the herring trade whose main demand is for “quality”—in other words, size. As the fish grow older they also increase in length up to a certain limit which varies according to locality. In the southern North Sea the maximum modal size of the oldest groups is about 27 cm., and the modal size of the young recruits to the shoal is 23–4 cm. (at four years of age), and as a year-class of herrings grows from four to seven or eight, we find that there is a change going on with regard to length between the above limits. A dearth of recruits in any year is followed by an absence of large fish a few years later, and conversely an abundance of young fish, such as was experienced in 1927 and 1928 (see Fig. 1), would lead to a large supply of large herrings in 1930.

Forecasting the herring stocks in the southern North Sea began in 1929, and so far the forecasts have been reasonably accurate, but it must be remembered that they are still in the experimental stage; nevertheless we hope that before long these prognostications will be issued with the same confidence as those which are broadcast daily by the Meteorological Office, and, once they are received with confidence by the trade, they should be of considerable financial value.

VI. SUMMARY.

Scale readings and size measurements enable the age distribution of herring shoals to be determined each year. By the analysis of this data it is possible to follow the fate of each year-class. The methods of sampling and of checking the statistical material are described, and the forecast and actual results for 1931 are compared, the agreement being close. Such forecasts enable the relative amounts of different year-classes to be forecast, though not the actual amount of the catch, since the latter depends on a number of factors such as gales, variable migration of fish, etc.

AN ECOLOGICAL RECONNAISSANCE IN WEST GREENLAND

By T. G. LONGSTAFF, D.M.

(With Plates VI-IX.)

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I. ACKNOWLEDGMENTS.

THE constitution and activities of the Oxford University Expedition to West Greenland in the Summer of 1928 have been briefly described, with maps and illustrations, in the *Geographical Journal* for July, 1929 (1). The collaboration of the Danish Administration, which has already been acknowledged, was essential to the success of our programme. The planning of an ecological survey in Greenland, and the working out of results afterwards, are greatly facilitated by the long series of papers published in the *Meddelelser om Grönland*.

We are greatly indebted to Prof. E. B. Poulton, F.R.S., Oxford, for getting the insect collections named by the experts whose papers are given in the list of references (2-9). The ecological data, including the flowers visited by insects, which are not published in this paper, are attached to the specimens in the Hope Department collection at Oxford. For the laborious task of analysing the contents of some 100 birds' stomachs and crops we are deeply indebted to O. W. Richards of the Department of Entomology in the Imperial College of Science. Finally I must record my great obligation to Charles Elton for his active help with this paper, without which I should never have accomplished my task.

An account of the vegetation by C. G. Trapnell will appear in the *Journal of Ecology* (10). With the assistance of Sir John Hanham he collected 125 Algae, 20 Fungi, 68 Lichens, 86 Bryophytes and 184 Phanerogams. He identified the

seeds and plants in the food of the birds, and the materials of their nests. All the botanical references in this paper are from his notes. Pollination, and the relation of manuring and feeding by animals to plant life, must be dealt with in another paper.

The collection of some 1400 insects, of 115 species, and the observations thereon were made by Major R. W. G. Hingston. The bird census was done by E. M. Nicholson, assisted by B. D. Nicholson and other members of the expedition. He has already published papers on the birds (11).

I have included some information on the distribution of the four commonest passerine birds from observations made in 1931 in 14 localities between Julianehaab (61° N.) in the extreme south, and Disko and the Inland Ice (69° N.) in the north.

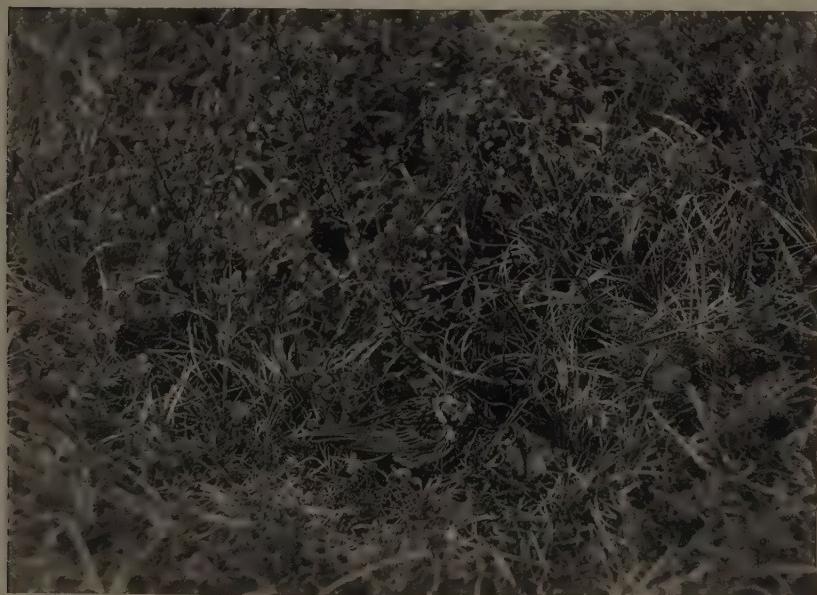
II. INTRODUCTION.

Our main idea was the ecological study and census of the land bird population. To find an area rich in land birds we had to avoid those parts of West Greenland where the ice-cap approaches the coast, and also the whole of the relatively sterile and mountainous coastal belt, which is subject to an unfavourable climatic régime. We sought a locality about half-way between the outer skerries and the Inland Ice, and therefore selected an area of low-lying rocky moorland adjoining the Kugssuk branch of the inner Godthaabs fjord system in $64^{\circ} 40'$ N. and $51^{\circ} 20'$ W., where the ice-free land is about 80 miles (130 km.) in breadth. Here, at a spot known as Isersiutilik, well removed from any human settlement, we camped and worked from June 16th to August 1st, 1928. Our working area was confined to about 8 square miles (20 sq. km.), and this will be alluded to in this paper as "the census area," to which all observations refer, unless otherwise stated. Probably we could not have selected a better spot for our particular purpose. But excursions farther inland showed that vegetation becomes more luxuriant as the climatic conditions become more continental. The optimum conditions for vegetation are found between the head of Kugssuk fjord and Ilulialik (1), as marked by the greater extent of stands of willow (*Salix glauca*) and the regular occurrence of alder (*Alnus incana*), both growing over 2 m. high in favourable sites. Still farther in, at Majuola, the proximity of the Inland Ice makes itself felt, and climatic conditions again become hostile, with deteriorating effects on the vegetation, although it is in precisely this locality that one of the twelfth-century Norse farmsteads are located. In reference to this it is interesting to note the report by Prof. Knud Jessen (12) on Trapnell's peat samples. His analyses indicate that the latest recession of the ice was accompanied by a climate appreciably warmer than at present, so that silver birch (*Betula pubescens*), now relict in the extreme south of Greenland, was able to flourish successfully 4° north of its present limits. This disposes of Ostenfeldt's suggestion that the silver birch was imported by the Norse settlers, and it lends some support to the hotly con-



Phot. 1. General view of heath and rocky moorland in centre of census area. Outer coast mountain range in background.

Photo. W. G. H. D. Crouch



Phot. 2. Lapland Bunting (*Calcarius lapponicus*) at nest among *Betula nana*, *Empetrum hermafroditum*, etc.

LONGSTAFF—WEST GREENLAND

Face p. 120

tested supposition that there has been some slight degeneration of climate during the historic period.

Our census area consisted of low-lying craggy moorland, with lakes and tarns occupying one-fifth of the area, and from which granite hills rise to 400 ft. (120 m.). To the north and south of our ground, hills rise to 2500 ft. (760 m.) and the size of the lakes increases. The high ground is littered with boulders left by the last recession of the ice, which must have covered the land in times geologically quite recent. In consequence the drainage system is immature and streams are small and little eroded, while the soil is very shallow.

III. ANIMAL AND PLANT COMMUNITIES.

The terrain is essentially moorland clothed with heath, which consists of a complex mosaic of different local dominants, with which smaller species may be specially associated. The different vertical layers of plants (ground, herb and shrub) form to some extent independent mosaics. A full account of the plant communities is being published elsewhere by Trapnell (10). He recognises a gradient in the character and luxuriance of the vegetation in the transect from the coast to the inland hills. Only the main divisions of the vegetation were used in the working out of animal communities, owing to the labour of collecting sufficient specimens to show minor variations in species and numbers; and even of these it must be remembered that the different types merge one into the other, and that the divisions are in fact somewhat arbitrary. It is very striking how little the animals fall into definite communities and how few habitats have exclusive species. For the study of animals in the field, the following subdivisions were employed: Heath, Willow Scrub, Rock Domes, Hummock Flats, Bog, Pools, Tarns and Lakes, Streams, and Shore-line.

The bird census concerned only the number of pairs breeding on the total area (a minimum of 728 pairs on about 8 sq. miles or 20 sq. km.). It is this figure which is quoted in the following tables, to give an idea of status. The birds cannot in fact be confined exactly to any one of our field subdivisions, but so far as possible each species is treated under its most characteristic habitat. The discussion of the food of birds and mammals is dealt with in section IV.

(a) Heath.

In describing this area Trapnell says (1, p. 65): "the vegetation about Isersiutilik varied remarkably, even every few yards, although the principal constituents of the flora were fairly constant. The ground had the appearance of a patchwork quilt of lichens, especially *Cladonia alpestris*, growing with mosses in dense mats among patches of dwarf shrubs. Of these, crowberry (*Empetrum nigrum* [= *hermaphroditum*]) is the most universally distributed, and provides a link with the inner fjord vegetation of Spitsbergen (13). Dwarf birch (*Betula nana*) is plentiful and the azalea-like *Ledum groenlandicum* often accompanies it. A bilberry (*Vaccinium uliginosum*) is common, and a small

form of it fruits abundantly on the stony ridges, where *Dryas integrifolia* is found, and, less frequently, *Rhododendron lapponicus*. In the deeper soil of hollows or valleys the grey willow (*Salix glauca*) forms copses a yard high." Trapnell has made a detailed study of the gradations in luxuriance of heath in different habitats, and includes willow scrub as the extreme type in this series. There is some peat (12). Though the soil is shallow, moth and fly pupae are frequent under the *Salix*-moss mat.

Table I. Animal community of heath (excluding willow scrub).

| MAMMALS. | | |
|----------------------|---|--|
| Reindeer | <i>Rangifer tarandus</i> | Not seen: formerly common |
| Arctic hare | <i>Lepus groenlandicus</i> | Droppings common; not seen on census area |
| Arctic fox | <i>Alopex lagopus</i> | Pair: droppings common |
| BIRDS. | | |
| Raven | <i>Corvus corax principalis</i> | 1 pair; and visitors |
| Lapland bunting | <i>Calcarius lapponicus groenlandicus</i> | 321 pairs (44 %) |
| Snow bunting | <i>Plectrophenax nivalis subnivalis</i> | 84 pairs (11.5 %) |
| Wheatear | <i>Oenanthe oe. leucorhoa</i> | 61 pairs (8.5 %) |
| Snowy owl | <i>Nyctea nyctea</i> | Straggler: hunting |
| Iceland falcon | <i>Falco rusticolus islandus</i> | Visitor: hunting |
| Peregrine | <i>F. peregrinus anatum</i> | Do. |
| Sea eagle | <i>Haliaetus albicilla groenlandicus</i> | Do. |
| Purple sandpiper | <i>Erolia m. maritima</i> | 20 pairs (2.75 %) |
| Arctic skua | <i>Stercorarius p. parasiticus</i> | 6 pairs (0.82 %) |
| Ptarmigan | <i>Lagopus mutus</i> | 28 pairs (3.8 %) |
| ARANEIDA. | | |
| Web spider | <i>Dictyna major</i> | Small irregular snares in leaves of <i>Betula nana</i> , <i>Ledum groenlandicum</i> , <i>Salix glauca</i> . White disc-shaped egg-bags often in folded leaf, contain about 20 eggs. For preys see this table |
| " | <i>Thanatus arcticus</i> | — |
| " | ? <i>Tetragnatha extensa</i> | Small webs on <i>Betula nana</i> |
| Hunting spider | <i>Lycosa hyperborea</i> | ♀ carries egg-bag in jaws |
| " | <i>L. glacialis</i> | — |
| " | <i>L. groenlandica</i> | — |
| " | <i>L. furcifera</i> | The most abundant spider. ♀ drags behind her the egg-bags, containing 80-90 eggs |
| " | <i>Hilaira frigida</i> | White spherical egg-bag under stones and lumps of moss |
| OPILIONIDA. | | |
| Hunting "harvestman" | <i>Mitopus morio</i> | Under stones, or, in good weather, hunting on heath. Less common than the Lycosids |
| ACARINA. | | |
| Mites | Not identified | Galls on <i>Betula nana</i> and <i>Potentilla tridentata</i> |

| DIPTERA. | | |
|--------------------------|---------------------------------------|---|
| Empid fly | Rhamphomyia hirtula | |
| " | R. nigrita | Caught by spider <i>Dictyna major</i> |
| Dolichopodid fly | Dolichopus groenlandicus | — |
| Hover fly | Platychirus hyperboreus | Visits flowers |
| " | P. albimanus | Visits flowers. Caught by spider <i>Dictyna major</i> |
| " | Melanostoma lundbecki | — |
| " | Syrphus torvus | Visits flowers |
| " | S. tarsatus | Visits flowers. Many specimens taken. Caught by spider <i>Dictyna major</i> |
| " | S. arcuatus | — |
| Bluebottle | Sphaerophoria scripta var. strigata | — |
| Fly " | Helophilus Groenlandicus | — |
| " | Calliphora uralensis | Lays eggs in excrement, dead animals, etc. |
| " | Phormia groenlandica | As last |
| " | Phaonia pallidisquama | Found visiting flowers |
| " | Lophoclees frenatus | — |
| " | Hydrotaea bispinosa | Found visiting flowers. Caught by spider <i>Dictyna major</i> |
| " | Limnophora arctica | Many specimens taken. Caught frequently by spider <i>Dictyna major</i> |
| " | L. hyperborea | — |
| " | Acroptena brunneifrons | Caught frequently by spider <i>Dictyna major</i> |
| " | Pegomyia tenera var. obscurior | — |
| " | Pegohylemyia profuga | Many specimens taken |
| " | Paregle radicum | Caught by spider <i>Dictyna major</i> |
| " | Fucellia intermedia | Stray from shore-line zone |
| Dung fly | Scatophaga squalida var. varipes | Numerous, visiting human excrement, in which eggs were laid |
| Crane fly | Tipula arctica | Common. Inconspicuous when at rest on heath |
| " | Helobia hybrida | — |
| Biting fly ("Black fly") | Simulium vittatum | Very numerous, biting man. Caught by spider <i>Dictyna major</i> |
| Mosquito | Aedes nigripes | Do. |
| Chironomid fly | Trichocladius variabilis | Caught by spider <i>Dictyna major</i> |
| " | Tanypterus pulchriventris | — |
| HYMENOPTERA. | | |
| Humble bee | Bombus arcticus } B. hyperboreus } | Frequent, especially above 500 ft. (c. 150 m.). Very abundant at 1000 ft. (c. 300 m.). Active through 24 hours. Queens seeking nesting sites in June. Visits flowers. Eaten by birds (see section IV) |
| Ichneumon | Cryptus arcticus | Abundant in second half of June, but not met with in July. Active in sunny weather |
| " | Barycnemis laeviceps | Under stones |
| " | Anilastus sp. | Seen in numbers probing entanglements of the spider <i>Dictyna major</i> . May lay eggs in cocoons |
| " | Cratichneumon aurivillii | — |

LEPIDOPTERA.

| | | |
|--------------------------|----------------------------|--|
| Fritillary butterfly | Brenthis chariclea arctica | Fairly abundant, sea-level to 2500 ft. (c. 765 m.). Gradually disappeared towards end of July. Often settles on green lichen. Strong flyer |
| Clouded yellow butterfly | Colias hecla | Fairly abundant, sea-level to 2500 ft. (c. 765 m.). Gradually disappeared towards end of July. Strong flyer |
| Moth | Anarta septentrionis | Day flying. Settled often on lichen patches harmonising with its own colours |
| " | A. leucocycla | Day flying. Swift on wing. Alights on lichens harmonising with its own colours (blue-grey). Visits flowers |
| " | Entephria polata brullei | Day flying |
| " | Eupithecia nanata gelidata | Day flying |
| " | Eremobia esculis | — |
| " | Pyrausta torvalis | Day flying |
| " | Sympistes lapponica | Settles on lichen patches harmonising with its own colours |
| " | Autographa parilis | — |
| " | Eumichtis sommeri | — |

NEUROPTERA.

| | | |
|------------|-------------------|------------------------------|
| Hemerobiid | Boromyia betulina | Common on <i>Betula nana</i> |
|------------|-------------------|------------------------------|

TRICHOPTERA.

| | | |
|------------|---------------------|---|
| Caddis fly | Limnophilus elegans | Aquatic larvae. Active at night only. Caught by spider <i>Dictyna major</i> |
| " | Apatania arctica | Aquatic larvae. Active only at night |

HEMIPTERA.

| | | |
|-------------|----------------------|---|
| Plant-louse | Myzocallis minimus | Common on stems and under sides of leaves of <i>Betula nana</i> . White egg-clump covered with brown scale is attached to birch stems |
| Coccid | Orthezia cataphracta | Frequent under stones, moss and lichen |
| " | Not identified | On <i>Carex rigida</i> (C.G.T.) |
| " | " | On <i>Betula nana</i> . C.G.T. found it in mats of white <i>Cladonia</i> |

COLEOPTERA.

| | | |
|---------------|--------------------------------|--|
| Ladybird | Coccinella transverso-guttata | On birch and willow. Seen once in web of spider <i>Dictyna major</i> |
| Weevil | Otiorrhynchus arcticus | Found only at Majuola |
| " | O. nodosus | Under stone |
| " | Phytonomus elongatus | Do. |
| Ground beetle | Patrobus septentrionalis | Under stones |
| " | Trichocellus cognatus ruficrus | In moss |
| Beetle | Byrrhus fasciatus | Under stones |

OLIGOCHAETA.

| | | |
|-------|----------------|--|
| Worms | Not identified | In one small area of <i>Empetrum</i> heath about 14 worms to 10 sq. ft. of moss and thin soil layer, over rock |
|-------|----------------|--|

Certain groups of animals were conspicuous by their absence. No specimen of ant, dragon-fly, earwig, cricket, cockroach, grasshopper, springtail, woodlouse, or terrestrial mollusc was taken anywhere on the heath in our area. The absence of springtails (*Collembola*) from the collections, which is confirmed by the examination of the birds' stomachs, needs confirmation, considering the great abundance of this group in arctic and temperate regions in a great variety of habitats. The scarcity of Chironomid flies is also striking.

The weather greatly influences the activity of a number of forms. Thus the ichneumon *Cryptus arcticus* used to hunt on sunny days, but retired under the heath in wet weather. The mating of the dung flies *Scatophaga squalida* var. *varipes* took place on sunny days after showers of rain. Eggs were laid in human excrement. On calm days, when the air was moist, the mosquitoes *Aedes nigripes* and the biting flies *Simulium vittatum* swarmed persistently about our heads. Spiders were also affected by weather: the abundant hunting spider *Lycosa furcifera* and the harvestman *Mitopus morio* hunted chiefly in sunny weather, hiding on wet days under lichen and moss, or stones.

The vegetarian animals on the heath in this area are the hare (and reindeer?), ptarmigan, and other birds partially, certain Diptera (e.g. crane flies), humble bees, butterflies and moths, Aphids and Coccids, and beetles. Beetles, however, were very scarce on the heath. The reindeer was abundant in earlier times though very scarce at the present day. Numerous traces of hares were seen, but the animals themselves were only seen outside the bird census area.

The carnivorous animals include the arctic fox, various "insectivorous" birds, predatory birds, spiders, certain Diptera (such as mosquitoes, biting midges, larvae of hoverflies), parasitic Hymenoptera, and ladybird beetles. The carnivorous Diptera are themselves eaten by spiders and birds, and the spiders by birds. Diptera outnumber all other orders both in number of individuals and species, and are the main agents in fertilising flowers. Large numbers of Lycosid spiders hunted over the heath, the most numerous being *Lycosa furcifera*. A count of eight entanglements of the spider *Dictyna major* produced 34 insects belonging to five species. The discussion of insects and spiders as the food of birds is reserved for section IV.

The dwarf birch (*Betula nana*), which in favoured spots forms somewhat scattered stands up to a metre high, amongst which the tall grass *Calamagrostis langsdorffii* is conspicuous, has a rather distinct animal community. The redpoll (*Carduelis linaria rostrata*) is a common breeder. Moths (such as *Anarta leucocycla*), caddis flies, and Chironomid flies, rest on the twigs and are concealed. Aphids are numerous on the birch, and are probably preyed on by larvae of Syrphid flies (*Syrphus* sp.) which were seen laying eggs on the leaves. The Hemerobiid *Boriomyia betulina* is also associated with the birch. An Argiopid spider spins a small snare in which small Diptera are caught. This species was not identified but may be *Tetragnatha extensa*.

(b) Willow scrub.

Willow scrub is included in Trapnell's heath series, but I must treat it separately. *Salix glauca* here grows up to a metre high. It forms dense thickets along the courses of those streams where humus is well developed in sheltered pockets on the moor, and at the foot of the low hills and in their shallow ravines. Apparently it can only flourish in sites protected by snow drifts in winter. In low damp sites it is associated with *Archangelica officinalis*, which was perhaps introduced by the early Norse settlers from their Kvan gardens in Iceland. This willow scrub harbours a fauna somewhat different from that of the typical heath. In 1931 I invariably found the redpoll (*Carduelis linaria rostrata*) wherever the willow scrub rose 18 in. or more above the surrounding vegetation, and this from Narsak (61° N.) and the 6 ft. willow forest of Ivigtut in the extreme south, to the 2 ft. scrub near the ice-cap (69° 50' N.) north-east of Disco. When I asked F. S. Chapman (of the Watkins Expedition) about the status of the redpoll in east Greenland, he replied that it was scarce and only found where Angelica was growing! The willow there was about 1 ft. high (i.e. not so obvious as Angelica).

Table II. Animals recorded from the willow scrub community.

| BIRDS. | | |
|------------------|-----------------------------------|---|
| Redpoll | <i>Carduelis linaria rostrata</i> | 149 pairs (20.5%). Nests in birch |
| ARANEIDA. | | |
| Web spider | <i>Dictyna major</i> | Small snares described in Table I |
| Crab spider | <i>Oxyptila dura</i> | Lies in wait for flies on female catkins |
| Hunting spider | <i>Lycosa furcifera</i> | Hunts in grass underneath scrub* |
| Web spider | <i>Tetragnatha extensa</i> | Small cartwheel snare about 4 in. in diameter. Catches small flies, mainly <i>Simulium</i> . Abundant where willows are high |
| ,, | <i>Araneus ocellatus</i> | Occurs only where willow is high. Web a foot across, set among long branches. Tendency for communal webs. Webs set to face the prevailing wind up ravines. Sometimes on rocks in willow ravines. Yellow disc-shaped egg-bag among leaves near web. 110–120 eggs |
| Large web spider | <i>A. quadratus</i> | Highly decorated spider. Lives in unusually luxuriant willow. Silk tent in willow leaves, leading to circular snare, 6–10 in. across |
| ACARINA. | | |
| Small red mites | Not identified | Found on ventral side of abdomen of <i>Simulium</i> |
| DIPTERA. | | |
| Empid fly | <i>Rhamphomyia nigrita</i> | — |
| ” | <i>R. hirtula</i> | — |
| Hover fly | <i>Melanostoma lundbecki</i> | Visits <i>Salix glauca</i> |

DIPTERA (continued).

| | | |
|--------------------------------|--|--|
| Hover fly (<i>continued</i>) | * <i>Platychirus hyperboreus</i> | Visits female catkins of willow for aphid excretions |
| " | <i>P. albimanus</i> | Do. |
| " | * <i>Syrphus tarsatus</i> | Visits male willow catkins. Seen to lay egg on leaves of willow, and in clefts between ovaries on catkins. In latter instance eggs placed among the clusters of aphids |
| " | <i>S. torvus</i> | <i>Syrphus</i> spp. found in webs of <i>Araneus ocellatus</i> and <i>A. quadratus</i> |
| " | <i>S. arcuatus</i> | " |
| " | * <i>Sphaerophoria scripta strigata</i> | — |
| " | * <i>Helophilus groenlandicus</i> | — |
| Fly | <i>Aphiochaeta groenlandica</i> | — |
| Bluebottle | * <i>Calliphora uralensis</i> | — |
| Carrión fly | <i>Phormia groenlandica</i> | — |
| " | <i>P. atriceps</i> | — |
| " | <i>Cynomyia mortuorum</i> | — |
| " | * <i>Phaonia pallidissima</i> | — |
| " | <i>Lophosceles frenatus</i> | Visits female catkins for aphid excretions |
| " | * <i>Limnophora arctica</i> | Abundant. Hides during strong wind. Found in webs of <i>Araneus quadratus</i> |
| " | <i>L. greyi</i> | — |
| " | <i>L. malaisei</i> | — |
| " | <i>Lispe uliginosa</i> | Visits female catkins for aphid excretions |
| " | * <i>Acroptena frontata</i> | Do. |
| " | <i>A. divisa</i> | — |
| " | <i>A. brunneifrons</i> | — |
| " | <i>A. verticina</i> | — |
| " | <i>Pegomyia tenera</i> var. <i>obscurior</i> | — |
| " | * <i>Pegohylemyia profuga</i> | — |
| " | <i>Paregle radicum</i> | — |
| " | <i>Delia fabricii</i> | — |
| " | <i>D. octoguttata</i> | — |
| Fungus gnat | * <i>Scatophaga squalida</i> var. <i>varipes</i> | Visits female catkins for aphid excretions |
| " | <i>Boletina groenlandica</i> | Taken by sweeping grass below willows |
| " | <i>Mycetophila fungorum</i> | Extremely numerous. Bites man, and seen sucking leaf-sap |
| Biting fly ("Black fly") | <i>Simulium vittatum</i> | Extremely numerous. Bites man. Found in webs of <i>Araneus ocellatus</i> and <i>A. quadratus</i> |
| Mosquito | <i>Aedes nigripes</i> | Abundant. Often sits along stems of willow. Found in webs of <i>Araneus quadratus</i> |
| Chironomid fly | <i>Chironomus hyperboreus</i> | Caught by sweeping grass below willows. Found in webs of <i>Araneus ocellatus</i> and <i>A. quadratus</i> |
| " | <i>Trichocladius variabilis</i> | |

(Species marked with * were found especially on flowers of *Archangelica officinalis*, as well as in the scrub.)

| | HYMENOPTERA. | |
|---------------------|--------------------------------|---|
| Humble bee | Bombus arcticus or hyperboreus | Visits female catkins of willow to get aphid excretions |
| Ichneumon | Orthocentrus repentinus | Found only at Majuola |
| " | Plectiscus arcticus | Do. |
| " | Phygadeuon sp. | Do. |
| " | Cratichneumon ? erythromelas | — |
| " | Banchus monileatus | Persistent visitor to flowers of <i>Archangelica officinalis</i> |
| " | Mesoleius groenlandicus | Persistent visitor to flowers of <i>Archangelica officinalis</i> (at Majuola) |
| " | Homotropus elegans nigritarsus | Almost certainly a parasite of larvae of hover flies (Syrphidae) (O.W.R.) |
| " | Hypamblys ? albopictus | Persistent visitor to flowers of Angelica |
| Saw fly | Pontania sp. | Galls found in willow leaves |
| | LEPIDOPTERA. | |
| Fritillary | Brenthis chariclea arctica | Visits female catkins of willow |
| Moth | Anarta septentrionis | — |
| " | A. leucocycla | — |
| " | Eumichtis sommeri | — |
| " | Eremobia esculis | In web of <i>Araneus ocellatus</i> |
| | TRICHOPTERA. | |
| Caddis fly | Limnophilus moestus | Aquatic larvae. Adults hide in scrub |
| " | L. miser | Do. |
| " | L. griseus | Do. |
| " | L. elegans | Do. |
| " | Apatania arctica | Do. |
| | EPHEMEROPTERA. | |
| May fly | Baetis sp. | Once in web of <i>Araneus ocellatus</i> |
| | HEMIPTERA. | |
| Plant-louse | — | Abundant on willow leaves, stems, and catkins |
| Bug | Nysius groenlandicus | Visits catkins of willow to get aphid excretions |
| | COLEOPTERA. | |
| Small ground-beetle | Bembidion grapei | — |
| Ladybird | Coccinella transverso-guttata | Larvae and adults eat aphids on <i>Salix glauca</i> leaves and catkins. Beetles become abundant in third week in July |

Two groups of insects are conspicuous in the animal community in willow scrub. First the swarms of resident and visiting Diptera, and secondly the colonies of Aphids on the willows themselves. Both groups form an important food supply for carnivorous animals (spiders, beetles, birds, etc.). The scrub teems with Diptera; mosquitoes, midges, and hover flies being the most numerous. *Aedes nigripes* (Pl. VIII, phot. 6) is an infernal pest, swarming round one's head in thousands. They did not penetrate below the upper canopy of the willow scrub, apparently owing to their preference for light: those entering our tents during daylight would always escape if a tiny opening was



Photo, T. G. Longstaff

Phot. 3. Pools, peat, and hummock flats from hills at the edge of census area.



Photo, W. G. H. D. Crouch

Phot. 4. General view of census area: hummock flats and pool in foreground,
rock domes on right.

made at the top, attracted apparently by the sunlight. The swarms are very sensitive to wind, which drives them to shelter. They attack man voraciously, and were seen buzzing round the ears of the arctic hare, and persistently attacking the eyelids of a young redpoll. In 1931, during the ascent of Hjortetakken, I was greatly troubled by mosquitoes on the snow up to a height of 2000 ft. (610 m.) but it is believed in West Greenland that the reindeer seek comparative relief from mosquitoes on the higher mountains during the summer. Mosquitoes are eaten by birds and spiders, and the larvae are probably eaten by fish. *Simulium vittatum* (the "black fly" of Canada), whose larva lives in running water, is also a great pest (Pl. VIII, phot. 6) and even more numerous than the mosquito. Hingston captured more than 60 in a single sweep of a net round his head, and at one time counted 75 resting on 2 sq. in. of a man's coat. When swarms of them collect round a tent the noise they make in alighting on the canvas is exactly like that of falling rain. They are sensitive to anything except a gentle wind, seeking shelter as soon as the wind is strong enough to blow a handkerchief out like a flag. As bloodsuckers they are less voracious than the mosquito. They also suck vegetable juices. Hingston watched them drawing sap from the stems and leaves of *Salix glauca*, which may therefore have an important relationship with the distribution of this pest. The presence of these two bloodsuckers in abundance forms an important difference between West Greenland and Spitsbergen where the black fly is absent, and the mosquito very rare even in the inner fjords. Chironomid flies (e.g. *Chironomus hyperboreus*) and Anthomyid flies (e.g. *Limnophora arctica*) were also common. Various Diptera, the bug *Nysius*, the humble bee, and the fritillary butterfly, were noticed visiting the willow Aphids for their excretions. The Aphids themselves are eaten by the ladybird and its larvae, and probably by the larvae of Syrphid flies. (*S. tarsatus* was seen laying eggs among the Aphid clusters, and the larvae of *Syrphus* are known to prey on Aphids.) Spiders are very numerous. A crab spider lies in wait for Diptera among the willow catkins. The Lycosid hunts on the ground. Web-spiders are conspicuous among the willows, there being three species not found on the heath (except possibly *Tetragnatha* on birch). These catch enormous numbers of insects, especially Diptera. The destructiveness of *Araneus ocellatus* is shown by the finding of the remains of 228 *Simulium* in a single snare 11 in. (28 cm.) in diameter. It will be observed from the above account of the community that the willow scrub is very closely interwoven with the insect fauna of this region. The few weeks at our disposal were only sufficient to give the merest impression of its ecological importance.

(c) *Rock domes.*

Rock outcrops, covered only with crustaceous and other lichens, show through the heath in many places. The Dolichopodid fly *Dolichopus groenlandicus* was found carrying out its courtship ceremony in these places. The

male pursues the female: they halt. Their heads come together. Then they separate and the male displays by a rapid raising and lowering of the wings. Certain flower-haunting hover flies (heath species) were noticed, while the young of a small bug, *Nysius groenlandicus*, were crawling over the bare rocks. *Lycosa groenlandica*, whose dark speckled colour rather resembled the black rock spotted with pale lichen, was also found. Many birds (ptarmigan, skua, Lapland bunting, snow bunting, and wheatear), also arctic foxes and hares (as shown by the presence of droppings, less commonly of hare than fox), visit these domes, which form good look-out posts. Thus the tops of some domes get covered with droppings and remains of food (such as bones, molluscs, feathers, etc.). With the accumulation of this manure and refuse a tuft of grassy vegetation develops (Pl. VIII, phot. 5), and a number of small animals are attracted to the spot, forming a scavenging community. Table III shows that the species are markedly different from those found generally on the heath, although the bare domes themselves show little peculiarity, only a paucity of species.

Table III. *Animal community of a rock dome hummock produced by manuring (one example investigated).*

| | | |
|--|-------------------------------|--|
| ARANEIDA. | | |
| Small spider | <i>Typhocrestus borealis</i> | Lives underneath droppings |
| Spider | <i>Thanatus arcticus</i> | — |
| ACARINA. | | |
| Black and red mite | Not identified | Numerous in fresh fox droppings |
| HYMENOPTERA. | | |
| Ichneumon | <i>Atractodes aterrimus</i> | Hunting among refuse |
| HEMIPTERA. | | |
| Small bug | <i>Nysius groenlandicus</i> | Abundant in fox and ptarmigan droppings. Scavenger; development takes place among refuse and droppings |
| " | <i>Chlamydatus pulicarius</i> | In grassy vegetation |
| COLEOPTERA. | | |
| Small ground beetle | <i>Bembidion grapei</i> | Uncommon; in moss |
| OLIGOCHAETA. | | |
| Several worms were dug from the soil of the hummock. | | |

(d) Hummock flats.

Flats covered with heathy hummocks, usually of *Empetrum* but maturing to *Betula* and *Ledum*, and quite different from the manured hummocks last mentioned, often occur on the moister parts of the moor (Pl. VII, phot. 3).

Trapnell considers that they occupy the site of the peat of the warm post-Glacial Period. The spider and insect community of these hummocks seems to differ but little from that of the heath in general, as may be seen from the following species that were collected: Araneida: *Dictyna major*, *Lycosa furcifera*; Diptera: *Dolichopus groenlandicus*, *Platychirus* sp., *Syrphus* sp., *Calliphora uralensis*, *Limnophora arctica*, *Piophila vulgaris*, *Simulium vittatum*,

Aedes nigripes, *Scatophaga squalida* var. *varipes*, *Chironomus* cf. *riparius*, *Tanypus pictipennis*, *Exechia frigida*, *Boletina groenlandica*; Hymenoptera: *Bombus* sp.; Lepidoptera: *Colias hecla groenlandica*, *Brenthis chariclea arctica*, *Eupithecia nanata gelidata*, *Entephria polita brullei*. *Sciara* sp. was bred out of peat from one of these hummocks. With the exception of the two Chironomid flies, which are clearly strays from the bog or aquatic communities, there is no species except *Exechia frigida* and *Sciara* sp. which was not found either on the heath or (as with *Boletina*) in the willow scrub. The conspicuous red flowers of willow herb (*Chamaenerium angustifolium*) are seldom visited by any insects except humble bees and Syrphid flies. The flies *Calliphora uralensis* and *Pio-philus vulgaris* came to carcasses of birds dragged amongst the hummocks by arctic foxes, while *Scatophaga squalida* was seen visiting bird droppings. A dwarf willow (*Salix glauca* var. *chloroclados*) is often covered with small galls caused by a mite. Amongst these hummocks the purple sandpiper (*Erolia m. maritima*) nests. The typical nesting site of the Lapland bunting (*Calcarius lapponicus groenlandicus*) is on the sides of those hummocks which are clothed with *Empetrum*, proximity to water being especially popular.

(e) Bog.

Bogs occur in many of the hollows on the moor. They range from typical cotton-grass bogs up to swamps with large open pools of water. The fauna of one bog investigated is given in Table IV.

Table IV. Animals found in a cotton-grass bog.

| BIRDS. | | |
|---------------------|---|--|
| Lapland bunting | <i>Calcarius lapponicus groenlandicus</i> | Catching insects |
| Rednecked phalarope | <i>Phalaropus lobatus</i> | Do. |
| ARANEIDA. | | |
| Hunting spider | <i>Lycosa furcifera</i> | (Common species on heath.) Hunts over grass and bog moss and surface of pools |
| Web spider | <i>Araneus groenlandicus</i> | (Common willow scrub species.) Web among grass leaves. One 6 in. web had four <i>Simulium</i> in it |
| DIPTERA. | | |
| Hover fly | <i>Syrphus</i> sp. | — |
| " | <i>Platychirus</i> sp. | — |
| Bluebottle | <i>Calliphora uralensis</i> | A few |
| Fly | <i>Limnophora arctica</i> | — |
| Black fly | <i>Simulium vittatum</i> | Occurs in myriads |
| Mosquito | <i>Aedes nigripes</i> | Swarms on calm days |
| Chironomid fly | <i>Chironomus hyperboreus</i> | — |
| " | <i>C. cf. riparius</i> | — |
| " | <i>Tanypus pictipennis</i> | — |
| " | <i>T. pulchripennis</i> | — |
| " | <i>Psectrocladius ? limbatus</i> | — |
| " | <i>Trichocladius variabilis</i> | — |

| | | |
|----------------------|----------------------------|---|
| | LEPIDOPTERA. | |
| Fritillary butterfly | Brenthis chariclea arctica | — |
| | TRICHOPTERA. | |
| Caddis fly | Limnophilus elegans | Abundant (with probably other species also). Hides in coarse grass. Larvae in the bog pools |
| | COLEOPTERA. | |
| Small water beetle | Hydroporus melanocephalus | In small and large bog pools |
| Ground beetle | Patrobus septentrionis | Found once in bog moss |
| | CRUSTACEA. | |
| Water-fleas | Cladocera | — |
| | MOLLUSCA. | |
| Snail | Limnaea sp. | — |

Diptera, especially the two blood-suckers *Aedes* and *Simulium* were very numerous. Caddis flies common. The two spiders take a heavy toll of the bog insects, including *Simulium* and Chironomid flies. The carnivorous plant *Pinguicula vulgaris* was also observed by Trapnell to have caught a number of the smaller insects (Diptera and Collembola), mites and even spiders. The presence of Collembola or springtails was not confirmed with specimens, and they were not otherwise obtained by the Expedition.

(f) Pools, tarns and lakes.

These include both bog pools and rock pools. The faunas were similar in a general way, but Mollusca and certain Crustacea appeared to be absent from the rock pools, whose bottoms were stony and not covered with decaying vegetation; the caddis flies may have been different species.

Table V. Animal community of pools.

| | | |
|----------------------|------------------------------|--|
| | BIRDS. | |
| Red-necked phalarope | Phaleropus lobatus | 24 pairs (3·3 %): nests beside bog pools |
| Mallard | Anas platyrhyncha conboscas | 11 pairs (1·5 %): nests beside bog pools |
| | TRICHOPTERA. | |
| Caddis flies | Not identified | Larvae crawl on bottoms of pools. In bog pools the cases made of straight stems, leaves, or a mixture; in rock pools cases made of sand |
| | COLEOPTERA. | |
| Whirligig beetle | Gyrinus opacus var. lecontei | Lives chiefly on surface |
| Small water beetle | Hydroporus melanocephalus | Numerous. Seen to kill Crustacea in a bog pool |
| Larger water beetle | Colymbetes dolabratus | Common. Keeps mainly to bottom, where it buries itself when alarmed. Seen eating a dead fish |
| | CRUSTACEA. | |
| | Not identified | Numerous |
| | MOLLUSCA. | |
| Snail | Not identified | — |



Photo. W. G. H. D. Crouch

Phot. 5. Rock dome rising from heath, with summit tuft of manured vegetation.

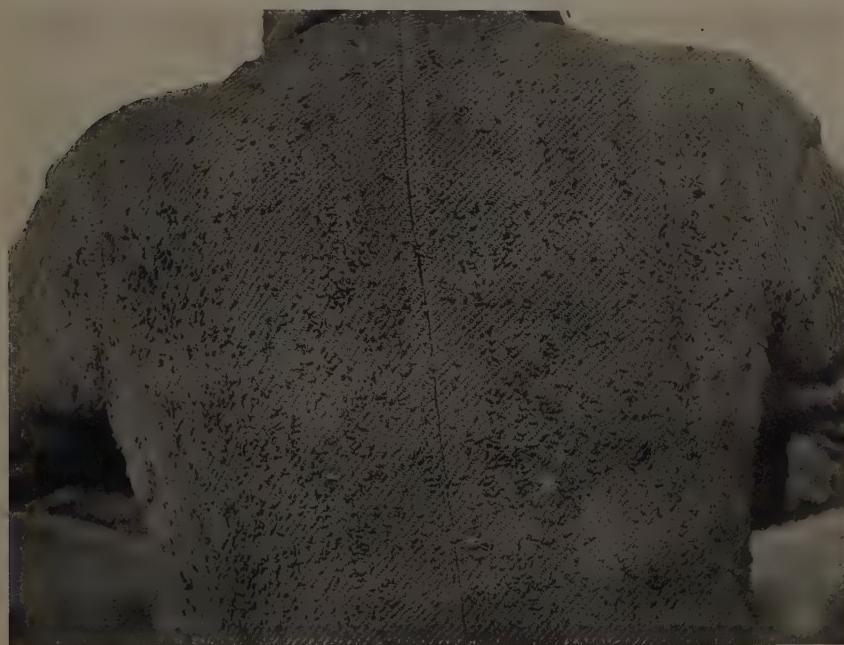


Photo. W. G. H. D. Crouch

Phot. 6. Mosquitoes (*Aedes nigripes*) and flies (*Simulium vittatum*) on Major Hingston.

LONGSTAFF—WEST GREENLAND

Small Diptera (e.g. *Helophilus groenlandicus*) are abundant around these bog pools. Mosquitoes continually alight on the surface, and *Simulium* visits them in large swarms. Contrary to anticipations, the larvae of small Diptera were seldom met with in the pools. Probably we were too late in the season to see any. No springtails (*Collembola*) were seen on the water surface or under stones, a surprising fact in view of their abundance in Spitsbergen. Neither were any found in birds' stomachs collected by the expedition.

The larger rock tarns and lakes, totalling about one-fifth of the census area, were not studied in detail. They evidently contain char (*Salmo alpinus?*), which probably forms the chief food of the red-throated diver (*Colymbus stellatus*) (6 pairs: 0·82 per cent.), the great northern diver (*Colymbus immer immer*) (2 pairs: 0·28 per cent.), and the red-breasted merganser (*Mergus serrator major*) (2 pairs). The white-tailed eagle (*Haliaëtus albicilla groenlandicus*) was occasionally seen hawking for them. The ice duck (*Clangula hyemalis*) (13 pairs: 1·8 per cent.) apparently does not feed on fish (v. section IV), but was found indiscriminately on tarns and lakes, as well as on the largest bog pools.

(g) Streams and stream margins.

The streams are small and uniformly shallow, floored with angular stones. Sea trout (*Salmo* sp.) entered one of them in fair numbers. Trapnell found the stickleback (*Gasterosteus aculeatus*), which he associates with Lyngema and lesser algae. The Lapland bunting, and to a lesser extent the snow bunting, haunts the margins.

The fauna of these habitats shows certain peculiarities. The streams themselves contain abundant Mollusca (not collected), planarian worms, and the larvae of the black fly *Simulium vittatum*. The latter curl themselves into a horseshoe shape and cling to the under surface of stones. Other insect larvae occurred but have not been identified.

The stream margin fauna was interesting. An Aphid (*Thripsaphis cyperi*) occurred abundantly in the grass, and with it was found the carnivorous larvae of the ladybird *Coccinella transverso-guttata*, which pupate about the third week of June, when many leave the grass and attach themselves to dry boulders along the margins of the streams. The small speckled hunting spider *Lycosa groenlandica* (also common on rock domes) comes on the rocks and hides beneath stones, while numbers of a scarlet mite and a larger grey and red species also occurred there. The small ground beetle *Bembidion grapei* comes under stones at the stream edge, and hover flies (*Syrphus*, *Platychirus* spp.) haunt the margin. Mosquitoes and *Simulium* are of course abundant. The small black bug *Nysius groenlandicus* occurs in heaps of decomposing vegetation. With the exception of the Aphid, the actual species were commonly found in various other habitats. The association is interesting, however, in indicating the possible importance of moisture for some of those forms which were not commonly found on the general heath (e.g. *Bembidion* and *Nysius*).

(h) Shore-line.

A distinct community of animals inhabits the drift-line which marks the limits of the highest tides and the winter-freezing pressure of the sea. Drift-wood, together with seaweed, cast up by the tide form a favourable shelter for certain forms. Conspicuous features of this zone are the overthrown patches of moss and heath, probably produced by the winter ice having lifted them and turned them over. I am confident that the cases of the extension of natural vegetation and peaty turf to below the level of high tides are sufficient to prove that the land is sinking at the present time: there is much corroborative evidence of this view from other parts of West Greenland. Small mussels (*Mytilus edulis*) are exposed on rocks at the lowest tides, and probably form part of the diet of the fox. At the head of the Kugssuk fjord, but beyond our area, there are extensive beds of *Zostera marina*, encrusted with Polyzoa (*Hippothoa hyalina*, etc.), which form the favourite feeding ground for flocks of mallard and merganser. Parties of immature redpolls (*Carduelis linaria rostrata*) visited the shore-line late in the season, while the snow bunting (*Plectrophenax nivalis subnivalis*) and the wheatear (*Oenanthe oe. leucorhoa*) were occasionally seen. A pair of turnstones (*Arenaria i. interpres*) was shot on passage, but with a 14 ft. (4 m.) tide this rocky shore was notably poor in waders and gulls.

Table VI. Animal community on the drift-line.

| | BIRD. | |
|------------------|--------------------------------------|--|
| Purple sandpiper | Erolia m. maritima | Commonest drift-line feeder |
| | | |
| | ARANEIDA. | |
| Spider | Drassodes signifer | Hunts at the water's edge |
| " | Oxyptila dura | — |
| " | Thanatus arcticus | — |
| Hunting spider | Lycosa groenlandica | Seen to capture <i>L. furcifera</i> |
| | L. furcifera | — |
| Spider " | Enoplognatha intrepida | — |
| " | Erigone whymperi | — |
| | OPILIONIDA. | |
| Harvestman | Mitopus morio | — |
| | | |
| | ACARINA. | |
| Mites | Not identified | Very numerous |
| | | |
| | DIPTERA. | |
| Hover fly | Helophilus borealis or groenlandicus | Visits edge of drift-line pools, and flowers. ♀ mates in air over sea-weed patches near high tide, and lays eggs on weed. Egg $\frac{1}{4}$ in. long, white, curved, attached at one end |
| Bluebottle | Calliphora uralensis | Breeds in cast up bodies of animals |
| Fly | Lophosceles frenatus | — |

| | | |
|---------------------|-------------------------|--|
| | | DIPTERA (<i>continued</i>). Scatophaga litorea var. nigripes |
| Dung fly | | ♀ mates on moist sea-weed patches at high tide, crawls in and lays eggs on weed, mates again out- side, and so on. Egg white, oval, $\frac{1}{4}$ in. long, fixed along- side in clusters on sea-weed |
| Fly | Scatella stagnalis | Abundant on wet decomposing vegetation |
| " | Piophila vulgaris | Do. |
| Black fly | Simulium vittatum | Very abundant |
| Mosquito | Aedes nigripes | Do. |
| Gnat | Trichocladus variabilis | — |
| | | HYMENOPTERA. Gelis terebrator |
| Ichneumon | | Wingless. Under stones, found only at Majuola |
| | | HEMIPTERA. Nysius groenlandicus |
| Bug | | Under stones |
| | | COLEOPTERA. Otiorrhynchus nodosus |
| Weevil | O. arcticus | Dead remains under stones Congregated under stones, found on site of old Norse settlement at Majuola |
| " | | |
| Beetle | Byrrhus fasciatus | Frequent under stones |
| Small ground beetle | Bembidion grapei | Do. |
| | | OLIGOCHAETA. Not identified |
| Worms | | Abundant under patches of sea- weed |

IV. FOOD OF BIRDS AND MAMMALS.

(a) Birds.

Note. Owing to the exigencies of the bird census work no collecting could be done on the census area until the last week of our stay. Hence most of the specimens were collected, with the assistance of H. P. Hanham, just outside the census area. In practically all cases the skins as well as the stomachs were preserved. These are in the British Museum (Natural History). The individual stomach analyses by O. W. Richards, numbered from these skins, will either be published in full elsewhere or deposited at the British Museum.

The bird census. A rough topographical map, on the scale of $3\frac{1}{2}$ in. to the mile, was made of the country around our base camp. On an area of about 8 sq. miles (20 sq. km.), of which one-fifth was fresh water, the Nicholsons located 728 breeding pairs. No part of our work was more laborious nor more conscientiously performed: but the figure of 91 pairs per sq. mile (= 1 pair to 7 acres) is of little value, as Elton has pointed out (16, p. 71). The density of individual species in their appropriate, and sometimes overlapping habitats, was far greater: it was greater than anything I have seen on any comparable English or Scottish moorland. Over large areas on the hummock flats of the *Empetrum* heath the density must have been at least one breeding pair per acre.

LAPLAND BUNTING (*Calcarius lapponicus groenlandicus*) 321 pairs: 44 per cent. (Pl. VI, phot. 2).

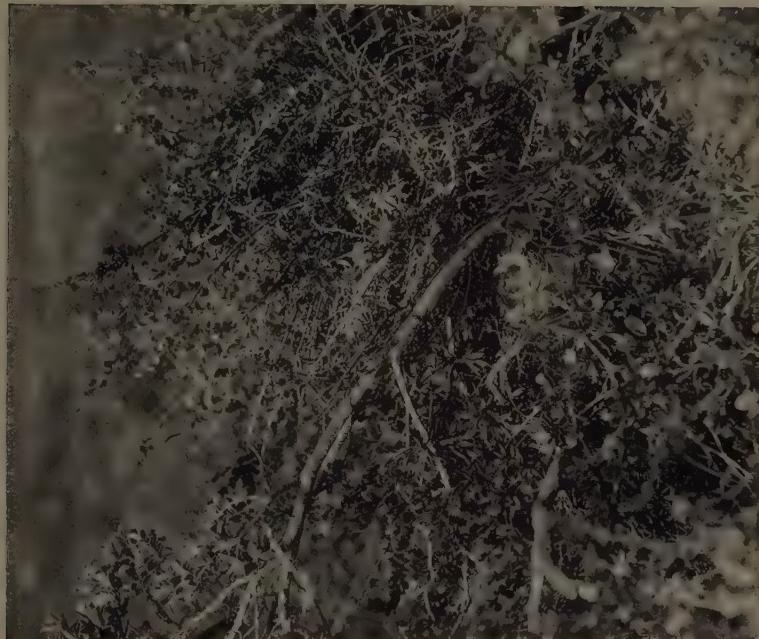
Of the fifteen specimens examined, one contained much vegetable matter, but no insects, and one contained much insect matter but no remains of plants. Diptera occurred in eleven cases, including Mycetophilinae, Chironomidae, Anthomyidae, Muscidae and larvae of Syrphidae. Beetles (Coleoptera) occurred in ten cases: of these, six cases contained eleven specimens of *Otiorrhynchus nodosus*, and four cases *Byrrhus fasciatus*; in three cases Curculionidae of two sp., and once *Coccinella transverso-guttata*. In four cases moths (Lepidoptera), spiders (Arachnida), and parasitic wasps (Hymenoptera, Ichneumonidae) were identified. Harvestmen (*Mitopus morio*), bugs and leaf-hoppers (Heteroptera, *Psylla* sp.) occurred twice. A lacewing (Neuroptera), *Boromyia betulina*, was found once. A snail (land Mollusca) was found in a specimen killed far up the fjord near Ivnajuagtok. Hingston frequently saw the Lapland bunting picking small Diptera from the "heath": and saw it capture the crane fly *Tipula arctica*. In nest material he found fragments of Diptera including *Platychirus albimanus*, *P. hyperboreus* and *Limnophora arctica*: also the spider *Lycosa furcifera* and a red mite. He watched it picking lice from its own feathers.

Out of the fifteen specimens all but one contained vegetable matter, in nine cases much. In two cases parts of flowers and buds were found. Of seeds, *Empetrum* was found in ten cases (up to twenty-eight in number). In only two cases were seeds of *Vaccinium uliginosum* identified (but this ripens late). Seeds of *Carex*, including *C. rotunda* and *C. glareosa* were found in three cases. *Juncus trifidus*, *Luzula* sp., and Cyperacea sp. each occurred once.

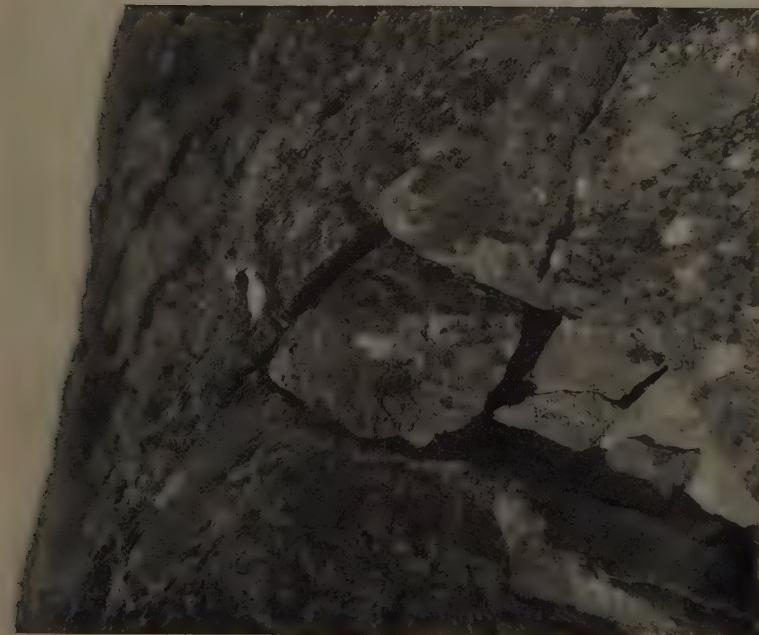
Summary. The Lapland bunting was by far the most numerous of all the birds on our census area, representing 52 per cent. of the total of the four common passerines. It feeds on a considerable range of both plants and insects. It becomes scarce at 500 ft. (150 m.). Its maximum density is on the wet hummock flats which are typical of so much of the low tundra country north of the tree limit. I correlate the closed *Empetrum* heath as an habitat indicator. Its northern limit is rather similar to that of *Mytilus edulis*. Its status as the commonest land bird in Baffin Island (14), on our census area, and on Kolghev (15), indicates that it would be the next bird to follow the snow bunting to Spitsbergen.

GREENLAND REDPOLL (*Carduelis linaria rostrata*) 149 pairs: 20·5 per cent.

Observation in the field suggested that the redpoll was chiefly a seed eater. They were watched feeding on *Oxyria digyna*, on seeds of grasses and sedges, on green seeds of *Cochlearia groenlandica*, and on catkins of *Salix glauca*. Utricles of *Carex rariflora* were found in a stomach and catkin buds of *Salix glauca* in a crop. Some seeds were found in ten of the thirteen stomachs preserved. Trapnell identified *Empetrum hermaphroditum* (= "nigrum") five times; *Hierochloe alpina* and *Carex glareosa* twice; *Stellaria humifera*, *Cochlearia groenlandica*, and Cyperaceae once each.



Phot. 8. Greenland Redpoll (*Carduelis linaria rostrata*) on nest among
Salix glauca, *Betula nana*, and *Ledum groenlandicum*.



Phot. 7. Male Snow Bunting (*Plectrophenax nivalis*) by nest crevice.
Photo. W. G. H. D. Crouch

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But examination of stomach contents proved that, during the breeding season, insects form a larger bulk of the food than seeds. Thus thirty-nine lice (Mallophaga) were found in one crop, and thirteen Lycosid spiders in another; in a stomach sixteen Diptera, and in another forty-three larvae. As regards the thirteen stomachs preserved numbers of insects were found in all but three. Of these ten stomachs six contained spiders (Arachnida, at least two sp.); five contained leafhoppers (Homoptera, *Psylla* sp.), once over 100 nymphs; four contained beetles (Coleoptera), caterpillars of moths (Lepidoptera, including Geometridae), and flies (Diptera, including Chironomidae, Muscidae, Anthomyidae, Mycetophilinae); three contained parasitic wasps (Hymenoptera, including cocoon of Cynipidae); and once lice (Mallophaga). Three of these stomachs came from considerably farther inland, but their contents are similar to those from the census area.

Nest material (six nests) is selected from the immediate site. It consists (1) of an inner lining of willow down (*Salix chlorooclados*) and/or white ptarmigan (*Lagopus mutus reinhardti*) feathers; (2) a thin layer of lichen, usually *Alectoria chalybeiformis*; (3) a main frame of *Calamagrostis langsdorffii* reinforced with dead twigs of *Betula nana*, *Salix* and *Ledum*.

Summary. During the breeding season the Greenland redpoll is dependent on a liberal supply of insect food, being particularly partial to spiders and leaf-hoppers. Both for food supply and for nesting sites it is attracted to stands of *Salix glauca*, or to the more rarely distributed stands of *Betula nana*. It was seen wandering up to 2000 ft. (600 m.) and twice nesting at 500 ft. (150 m.). In 1931, from the 6 ft. thickets of Ivigtut in the extreme south to the 2 ft. patches on Disko in the north, through 8° of latitude, I found it wherever the grey willow (*Salix glauca*) grew 1 ft. above the surrounding vegetation. The growth of such vegetation is dependent on protective snow covering during the winter. The redpoll's roving habit of flight would assist it to find a few snow-free areas in West Greenland, where it can subsist through the winter on seeds, as it does to some extent during the summer.

SNOW BUNTING (*Plectrophenax nivalis subnivalis*) 84 pairs: 11·5 per cent.

Hingston notes that with us the snow bunting was largely a seed eater; while Summerhayes and Elton (13) state that in North-East Land (Spitsbergen) the distribution is limited mainly by presence or absence of Chironomid flies. The analysis of fifteen stomachs by O. W. Richards proves the bird to have a very varied diet. With the exception of one shot on Ilulialik hill, all proved to contain animal as well as vegetable food. Of the animal food single instances were several shells of a Gasteropod (Mollusca), moth (Lepidoptera), spider (Arachnida), harvestman (Phalangida) *Mitopus morio*, mite (Acarina) and two Gamasidae sp. Bugs (Heteroptera) occurred in four cases, three being *Nysius groenlandicus* with up to thirteen individuals. Parasitic wasps (Hymenoptera) occurred in five cases, represented by Ichneumonidae, one Ophioninae

and one Chalcidoidea. Beetles (Coleoptera) were identified in nine cases, including *Otiorrhynchus nodosus* in three cases, Curculionidae in two cases, and *Byrrhus fasciatus* once. Flies (Diptera) occurred in ten cases, including Chironomidae, Tipulidae and *Sciara* sp. Hingston took from mouth the spider *Lycosa furcifera* and found *Dictyna major* being carried to the young, as also the crane fly *Tipula arctica*. He took from bills of birds shot an Ichneumon of *Phygadeuon* sp. and the flies *Limnophora arctica* and *Pegohylemyia profuga*. Trapnell reports that stomach contents show a great mixture of seeds often difficult of determination. All fifteen stomachs contained vegetable matter, half of them a large quantity of indeterminate material. The commonest seed was that of *Empetrum hermaphroditum* (= "nigrum")—nine cases, in one of which fifty-one seeds were counted. Flowers and seeds of *Vaccinium uliginosum* were identified in three cases; Polygonaceae in six cases, *Polygonum viviparum* and *Rumex acetosella* being identified. In seven cases *Carex*, including *C. glareosa*, *C. rariflora*, and *C. rigida*. In one case *Juncus trifidus*. Of the Caryophyllaceae, *Stellaria longipes* twice and *S. humifera* once. Single occurrences were—*Pedicularis* sp., *Eriophorum angustifolium*, *Cerastium alpinum*: Cruciferae, *Draba nivalis*, *Cochlearia groenlandica*: Cyperaceae, *Scirpus coespitosus*. Of mosses *Polytrichum juniperinum* occurred four times and unidentified fragments twice.

Summary. The snow bunting is the most omnivorous of the four common passerines of West Greenland. I suggest that this is the factor which accounts for its distribution extending from the Scottish Highlands to the most northerly lands. In West Greenland it breeds amongst broken rocks or scree with open vegetation at any altitude from sea-level up to at least 2300 ft. (700 m.).

GREENLAND WHEATEAR (*Oenanthe oenanthe leucorhoa*) 61 pairs: 8·5 per cent.

We only had seven specimens for analysis by Richards, with another (fledged nestling No. 61) by Hingston from Ilulialik, 1800 ft. (550 m.). Of beetles (Coleoptera) and their larvae seventeen specimens were found in six out of the eight cases; including nine specimens of *Otiorrhynchus nodosus* from three stomachs; *Otiorrhynchus arcticus*, *Byrrhus fasciatus*, *Colymbetes dolabratus* and a weevil sp., besides a species not in our collection. Hingston found several *Byrrhus fasciatus*, *Otiorrhynchus arcticus*, and a Carabid in nests. Several times he noted birds digging pupae and beetle larvae out of the ground. Two of my specimens have the upper surface of the beak bruised and scarred, apparently from digging in rock crevices. Parasitic wasps (Hymenoptera) are represented by seventeen specimens from six out of the eight stomachs examined. These include ten specimens of at least two species of Ichneumonidae not in our collections, but these birds were collected at some distance from our census area (skin Nos. 16, 38, 115, 116). Other Ichneumonidae include two Cryptinae (one *Cryptus arcticus*) and one Pimplinae. There is one sawfly (Nematinae) and a Serphid. Flies (Diptera), including larvae, are represented

by twenty specimens from five stomachs. *Tipula arctica* and an Anthomyiid were found twice; *Scatophaga* sp. once; and Syrphid and other larvae in two stomachs. Birds were habitually seen at the latrines feeding on dung flies and their grubs, especially *Scatophaga squalida*. E.M.N. records them snapping up the mosquito *Aedes nigripes*. From observation he calculates that a pair will account for 100,000 insects during the breeding season. But the fact that it preys so much on the parasitic wasps makes it extremely difficult to estimate its real effect on insect life. Moths (Lepidoptera) were found in two stomachs and their caterpillars in two others. Hingston considers the bird to be a serious enemy of moths, having found more than one species in nests. Of the bug (Heteroptera) *Nysius groenlandicus*, forty-one individuals were found in two stomachs. Single identifications were: lacewing (Neuroptera) *Boromia betulina*, caddis fly (Trichoptera) *Limnophilus miser*, and harvestman (Phalangida) *Mitopus morio*. Spiders only occurred twice in the eight stomachs. But Hingston identified *Lycosa furcifera* from the mouth, and found four and three and one of same in nests. The humble bee *Bombus arcticus* occurred once (No. 61). Two gastropod shells were found in an island specimen (No. 16) and a sea shrimp in a nest at Ilulialik 1800 ft. (550 m.).

Plant food was almost limited to seeds, six stomachs containing up to fifty seeds of *Empetrum*; *Vaccinium uliginosum* (fifty-six seeds) and ? *Juniperus communis* (three seeds) were each found in two stomachs. Very little other vegetable material was ever found. In one stomach there were no plant remains.

Two nests indicated no system of selection for nesting materials, which are taken from the most diverse habitats. The inner lining consisted chiefly of *Calliergon sarmentosum*, with fragments of *Cetraria hiascens*, *Sphagnum girgensohnii* and *Alectoria* sp. The outer casing is chiefly heads and roots of grasses, with *Calliergon sarmentosum*, *Drepanocladus fluitans*, *Rhacomitrium fasciculare*, *R. hypnoides*, *Cetraria hiascens*, and *Cladonia* sp.

Summary. The Greenland wheatear is more carnivorous and less vegetarian than either of the other three small passerines. It is very partial to beetles, larvae, and grubs which it picks out of detritus soil and rock crevices where the vegetation is open. It nests up to 1800 ft. (550 m.). I have found it (1931) scarce on the outer coast and islands, but numerous on the mainland even up to nearly 70° N. It is confined to a definite type of rocky territory, especially cliffs and "boiler plates," large not broken rock exposures, which may account for its reported rarity in Baffin Island (14); obviously it cannot exist beyond the limits of a rather special insect supply, and is of necessity completely migratory.

PTARMIGAN (*Lagopus mutus reinhardtii*) 28 pairs: 3·8 per cent.

Many faeces together with nine fresh crops were examined. *Empetrum* leaves, berries, and seeds were always present in large quantities, *Empetrum* seeds forming 80 per cent. of stomach contents in four cases. Next come leaves

of *Salix glauca*. Then leaves, flowers, unripe and ripe berries and seeds of *Vaccinium uliginosum*. In half of the specimens leaves and catkins of *Betula nana* were found. Leaves of *Polygonum viviparum* and *Pedicularis*, tips of *Equisetum arvense*, *Cladonia* sp., and utricles of *Carex* were identified once each. *Empetrum hermaphroditum* fruits from mid-June to the end of August, thus providing a continuous food supply, unlike *Vaccinium uliginosum* which fruits only late in July.

REDNECKED PHALAROPE (*Phalaropus lobatus*) 24 pairs: 3·3 per cent.

All thirteen specimens analysed contained insects, in large numbers except in two cases. In five cases masses of insect remains could not be identified. Flies (Diptera) and their larvae, were identified in eight cases: these included Mycetophilidae in six cases, with *Sciara* sp. and Macrocerinae; Anthomyidae of two spp. five times; Chironomidae twice, and in one case over 200 larvae; Tipulidae twice; Tachinidae, *Calliphora*, once; Nematocera pupae once. Beetles (Coleoptera) and their larvae occurred in nine cases: including *Otiorrhynchus nodosus* thrice; *Colymbetes dolabratus* twice; *Patrobus septentrionis*, and *Byrrhus fasciatus*. Parasitic wasps (Hymenoptera) occurred in five cases; including numerous Ichneumonidae with *Plectiscus* sp. and *Stenomacrus* sp.; Cynipidae, probably Eucoelinae, twice; and Chalcidoidea. The bug (Heteroptera) *Nysius groenlandicus* was found in four cases. Aphid (Homoptera) twice, including Pemphiginae sp. Mites (Acarina) twice. Spiders (Arachnida) twice. A large moth (Lepidoptera), a caddis fly (Trichoptera) *Limnophilus miser*, a lacewing (Neuroptera) *Boromia betulina*, and shells of a gasteropod once each. Of the thirteen specimens examined only one contained much vegetable matter; six contained single seeds, twice of *Hippuris vulgaris*; six contained no vegetable matter.

A nest consisted chiefly of the leaves of two bog plants, *Salix chloroclados* and *Carex rariflora*. Several were found nesting in territories of ptarmigan, which insures defence from attacks of skuas (*Stercorarius p. parasiticus*) (11).

PURPLE SANDPIPER (*Erolia maritima maritima*) 20 pairs: 2·75 per cent.

Only three specimens obtained, and of these only one (No. 41) a chick, gave good material. All contained shell fragments (Mollusca: once Gastropoda). All contained insects. Flies (Diptera) included Chironomidae spp., *Sciara* spp., *Aphiochaeta* sp., and Anthomyidae. Parasitic wasps (Hymenoptera) included Cynipidae (Eucoelinae), Serphidae, and Ichneumonidae (Cryptinae). Beetle (Coleoptera) *Otiorrhynchus nodosus* was found twice. Bug (Heteroptera) *Nysius groenlandicus*, Aphid (Homoptera), and spider (Arachnida) once each. Of plant food only one to five seeds were found, including *Empetrum*, Cyperaceae, *Ranunculus confervoides*, a bulbil of *Saxifraga cernua* and a moss capsule. Hingston reports it picking small diptera from the heath; taking *Scatophaga squalida* and its larvae at the latrines; catching insects and spiders at the brink of pools; and feeding on insects and worms under cast up sea-weed at the drift-line.

LONGTAILED DUCK (*Clangula hyemalis*) 13 pairs: 1·8 per cent.

Only two specimens available. One contained beetle (Coleoptera) *Colymbetes dolabratus* and the other larvae of a water beetle. One had Diptera, *Simulium* and *Sciara* sp. The other remains of Crustacea. One had a plant bud and a capsule of *Polytrichum*.

MALLARD (*Anas platyrhynchos*) 11 pairs: 1·5 per cent.

Colymbetes dolabratus was taken from an adult's stomach and eighty seeds, mainly *Empetrum*, from a duckling.

ARCTIC SKUA (*Stercorarius parasiticus*) 6 pairs: 0·82 per cent.

In pellets were found flowers of *Vaccinium uliginosum* common: numerous seeds, some of Cyperaceae: one *Empetrum* berry: small fragments of grass, moss, and lichen: small leaves of an evergreen plant. It is parasitic on fishing gulls and terns, and is known to devour eggs and nestlings freely.

RAVEN (*Corvus corax principalis*) 1 pair: 0·1 per cent.

A carrion feeder. Phalarope chick found in a casting: probably takes eggs as well as young birds. Hingston considers it the chief enemy of *Bombus arcticus*; pupae in castings prove that it eats bees' nests. The large crane fly *Tipula arctica* was also found in a casting. Seeds of *Juniperus communis* and *Empetrum* were found regularly in faeces.

(b) *Mammals.***FOX (*Alopex lagopus*).**

One pair on our census area, another on neighbouring island. Almost certainly responsible for collections of mussel shells (*Mytilus edulis*), sea-urchins and starfish (*Echinoderma*) found on prominent manured turf hummocks, the same remains together with bones of fledglings being found in droppings. A dropping from Ilulialik 1800 ft. (550 m.) contained hare fur. Trapnell found droppings which consisted almost entirely of berries of *Empetrum hermaphroditum* and juniper. Scattered along the coast were innumerable wings and skins of razorbills (*Alca torda*), said by Greenlanders to be a principal source of winter food supply, the foxes catching the birds on the sea ice and beside small openings.

HARE (*Lepus groenlandicus*).

Although the hare was not seen actually on our census area, we found many droppings. Two were seen at 500 ft. (150 m.) just off our area, and at 2000 ft. (600 m.) at Ilulialik. It is possible that they seek the hills in summer time to get away from the plague of mosquitoes and black fly. Trapnell reports droppings mainly found on patches of *Alectoria* or *Salix herbacea* communities, characteristic of the upper zone of the heath, they consist mainly of woody tissues of stems and roots of *Salix herbacea*, *Empetrum hermaphroditum* and probably *Betula*

nana; *Carex* heads are frequent, including *C. rigida* and *C. glareosa*; some fragments of sedge and grass glumes, and seeds, berries and leaves of *Empetrum*.

REINDEER (*Rangifer tarandus*).

Not met with on our census area, but old antlers common. Tracks in snow on Ivisat at 2000 ft. (600 m.). I attribute old game paths across "passes" to the former vast herds, which were nearly exterminated during last century. The survivors seek the hills in summer time, probably to escape mosquitoes. May have profoundly affected the vegetation in the past, but not now.

V. SUMMARY.

By investigating conditions in a somewhat lower latitude we endeavoured to extend the work of the Oxford parties in Spitsbergen (13) in the direction of getting a picture of ecological conditions in Britain during the close of the last Glacial maximum.

A pioneer ecological survey was made over 8 sq. miles (20 sq. km.) in a climatically favourable part of the Godthaab district of West Greenland. Owing to the patchwork character of the vegetation it proved difficult to separate the animals and plants into definite communities, indicating that the marked zonation of the high arctic quickly breaks down at lower latitudes.

Nevertheless an attempt is made to describe certain animal and plant communities. The diet of the commonest birds is described. A census was made of breeding pairs.

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SOME FACTORS INFLUENCING THE DISTRIBUTION OF CERTAIN PROTOZOA IN BIOLOGICAL FILTERS

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I. INTRODUCTION.

DURING the past four years investigations have been carried out to discover whether the principle of biological purification on percolating filters could be applied to the waste effluent from the beet sugar factories. At an early stage in the research it was found that large numbers of Protozoa, as well as bacteria and other organisms, were inhabitants of such filters. At first the work was done on a large scale at a factory, but when it was transferred to the laboratory with specially designed filters (1) it was thought of interest to make frequent observations of the protozoan species, since opportunity would thus be afforded for studying the effects of changes in hydrogen-ion concentration and in chemical composition of the medium on the fauna. Knowledge of the ecology of Protozoa has mostly been derived from the study of inland waters and soil, where the conditions could not be varied at will, or from culture solutions under laboratory conditions. In the filters, on the other hand, which depend for their population on chance contaminations and therefore approximate to natural conditions, the medium can be changed at will and therefore a good opportunity is afforded for work of this type.

Records have been kept of the following types of Protozoa occurring in the filters, and as, in some cases, the species have not been identified only the generic names are included in the list.

| Sarcodina | | Mastigophora | | Ciliata | |
|---------------|----------------|---------------|----------------|--------------|----------------|
| Genus | No. of species | Genus | No. of species | Genus | No. of species |
| Amoeba | 3 | Bodo | 2 | Colpoda | 2 |
| Vahlkampfia | 2 | Heteromita | 2 | Colpidium | 2 |
| Naegleria | 1 | Cercomonas | 1 | Glancomona | 2 |
| Hartmanella | 1 | Oicomonas | 1 | Chilodon | 2 |
| Sappinia | 1 | Trepomonas | 1 | Paramoecium | 2 |
| Pelomyxa | 1 | Proleptomonas | 1 | Lionotus | 2 |
| Arcella | 1 | Astasia | 1 | Vorticella | 2 |
| Hyalosphenia | 1 | Entosiphon | 1 | Pleuronema | 1 |
| Euglypha | 1 | | | Histro | 1 |
| Cochliopodium | 1 | | | Spathidium | 1 |
| | | | | Oxytricha | 1 |
| | | | | Uroleptus | 1 |
| | | | | Epistylis | 1 |
| | | | | Podophrya | 1 |
| | | | | Cinetochilum | 1 |

In this paper only the following species have been considered as regards the effect of the varying conditions: *Bodo saltans* Ehrbg., *Trepomonas agilis* Dujardin, *Arcella vulgaris* Ehrbg., *Colpidium colpoda* Stein, *Paramoecium putrinum* Clap. and Lach., *Pleuronema chrysalis* Ehrbg., *Cinetochilum margaritaceum* Ehrbg., *Lionotus fasciola* Ehrbg.

II. METHODS.

The object of the experimental filters was to convert a 0·2 per cent. solution of sucrose into carbon dioxide and water in the shortest possible space and time. Each filter consisted of six earthenware pipes each 12 in. long by 4 in. diameter; these were arranged in vertical series, each separated from the next by a space deep enough to allow of sampling the effluent from each section. The filters were filled with gravel ($\frac{1}{4}-\frac{3}{8}$ in.=0·6-1 cm.), and the sections were seeded with some of the film obtained from larger experimental filters which had been working at the Colwick factory of the Anglo-Scottish Beet Sugar Corporation for two years, and which therefore contained a representative fauna and flora. The filters were fed with about 5 litres of solution in 24 hours from an aspirator fitted with a Mariotte's constant head device. The solution unless otherwise stated had the following composition:

| | | | | | |
|---|-----|-----|-----|------|-----------|
| Sucrose | ... | ... | ... | 0·2 | per cent. |
| NaCl | ... | ... | ... | 0·03 | , |
| K ₂ HPO ₄ | ... | ... | ... | 0·03 | , |
| KH ₂ PO ₄ | ... | ... | ... | 0·02 | , |
| MgSO ₄ | ... | ... | ... | 0·01 | , |
| (NH ₄) ₂ SO ₄ | ... | ... | ... | 0·03 | , |
| CaCO ₃ | ... | ... | ... | 0·03 | , |

A record was kept of the changes in acidity in each section and of the purification, as evidenced by the test for dissolved oxygen taken up in 5 days, which is a measure of the amount of reducing material present in the solution (3).

The decomposition of carbohydrates and ammonia in their passage through the filters is roughly as follows (1, 2): in the first section the greater part of the sugar is converted into various organic acids, among which lactic, pyruvic, acetic and formic may occur; in the second and third sections these acids undergo oxidation, and in the fourth, fifth and sixth sections practically no carbohydrates are present; the ammonia disappears after the first section and amino acids are built up in the second section and to a lesser extent in the third; in the fourth section ammonia appears again from the amino acids and this is subsequently converted into nitrites and nitrates. Crudely therefore the sections may be classified as follows:

1. Organic acids, pH under 7·0.
2. Amino acids, pH under 7·0.
3. Amino acids decreasing, pH about 7·0.
4. Amino acids decreasing, appearance of nitrites and nitrates, pH over 7·0.
5. Very little organic matter, appearance of nitrites and nitrates, pH over 7·0.
6. Very little organic matter, appearance of nitrites and nitrates, pH over 7·0.

III. RESULTS.

The five principal factors which may be involved in determining the protozoan distribution are: hydrogen-ion concentration, purification, food supply, direct chemical action, and lastly the presence of large numbers of particular bacteria, developing in the solution in response to the presence of certain chemical substances.

Purification. As judged by the five-day tests the percentage of oxidisable material decreased from the top of the filter (section 1) down to the bottom (section 6), and to discover what effect this had on the Protozoa observations were made on the various sections. The percentage of occurrences of the different species of Protozoa varied with the different levels of the filter as is seen from Table I. In this table the percentage occurrences were calculated on the total number of observations made, that is the total number of times the organism might have occurred, in each section. The figures quoted in the tables bear no reference to the relative abundance of the animals on any one day, since presence or absence alone were recorded. It is difficult in such material to estimate actual numbers with any degree of accuracy, but under exactly similar conditions the numbers fluctuate to a very marked extent.

Table I. *Distribution of the species of Protozoa through the filters.*

| | Section 1 | | Section 2 | | Section 3 | | Section 4 | | Section 5 | | Section 6 | |
|---------------|-----------------|------------|-----------------|------------|-----------------|------------|-----------------|------------|-----------------|------------|-----------------|------------|
| | No. of cases | % rence |
| Bodo | 275 | 39·6 | 273 | 36·9 | 273 | 34·4 | 271 | 29·9 | 265 | 28·8 | 270 | 26·3 |
| Trepomonas | 244 | 36·9 | 250 | 40·0 | 247 | 28·7 | 245 | 21·2 | 249 | 17·6 | 245 | 14·3 |
| Colpidium | 274 | 64·6 | 274 | 74·4 | 274 | 59·1 | 274 | 58·0 | 274 | 39·0 | 274 | 27·0 |
| Paramoecium | 262 | 67·1 | 266 | 80·1 | 267 | 80·5 | 266 | 78·5 | 266 | 69·9 | 267 | 62·9 |
| Pleuronema | 271 | 56·1 | 270 | 61·5 | 270 | 69·6 | 270 | 54·1 | 270 | 45·2 | 270 | 41·1 |
| *Arcella | 162 | 11·7 | 162 | 22·8 | 162 | 40·7 | 162 | 67·6 | 162 | 71·2 | 134 | 72·4 |
| *Cinetochilum | 148 | 21·6 | 148 | 27·0 | 148 | 43·9 | 148 | 68·9 | 148 | 69·9 | 112 | 65·2 |

* These two species differ from the rest in that they were not present in all filters and the results for the periods when they were known not to occur have been omitted.

It will be noted that the protozoan species can be divided into three groups, firstly those like *Arcella* and *Cinetochilum*, which prefer the lower levels of the filter, secondly those like *Trepomonas*, *Colpidium* and *Bodo*, which are found mostly in the upper layers; and thirdly those which are comparatively indifferent, like *Paramoecium* and possibly *Pleuronema*.

This distribution is undoubtedly influenced by two main factors: the purity of the medium, and the food supply. *Cinetochilum* which feeds on organic débris, small organisms and bacteria (4) could undoubtedly obtain a more adequate food supply higher in the filter; it is therefore clear that it requires an environment relatively free from soluble organic compounds and so is limited in its range by the conditions of the effluent. On the other hand it is very problematical whether *Colpidium*, which feeds almost exclusively on bacteria (4, 5), could obtain a living in the bottom sections, where the

bacterial flora is greatly reduced, quite apart from any considerations of the purity of the medium, and so in this case the food supply is possibly the limiting factor. This was borne out by observation, for the animals in the lower sections were small and obviously starved.

Further information on these points was obtained when the filters were receiving only tap water. During this period *Colpidium* and *Bodo*, which commonly occur at the top, were reduced in numbers, while the percentage of occurrences of *Cinetochilum* changed from 10·7 in the sucrose solution to 65·5 in the tap water. The percentage occurrence of *Paramoecium* was comparatively unchanged (Table II).

Table II. Percentage occurrences of species during 14 days with sucrose solution and 14 days with tap water, all sections added together.

| Species | Total No. of observations | 0·2 % sucrose | Tap water |
|-----------------------------------|---------------------------|---------------|-----------|
| <i>Paramoecium putrinum</i> | 84 | 77·4 | 82·1 |
| <i>Cinetochilum margaritaceum</i> | 84 | 10·7 | 65·5 |
| <i>Colpidium colpoda</i> | 84 | 77·4 | 19·1 |
| <i>Bodo saltans</i> | 84 | 78·6 | 17·8 |

Effect of pH values. The pH values in the various sections of the filters ranged from 4·3 to 8·0; the acid conditions being found more often in the first two sections. Tables III-IX have therefore been prepared from separate sections, so as to eliminate other variables, such as purification, as far as possible. The majority of the Protozoa found are able to live throughout the range of pH values, provided they are not adversely affected by other conditions, such as impurity, though in many cases the low or high pH values have a limiting effect. As the behaviour of the species is different, consideration of each one individually is necessary.

Trepomonas. As is seen in Table I this species is not an ubiquitous inhabitant of the filters; but when it does occur its distribution is largely affected by the purity of the solution. The pH values *per se* have no marked effect (Table III).

Colpidium. Here again the distribution is little affected by pH values though there is some evidence that neutrality or slight alkalinity are the most suitable conditions (Table IV).

Paramoecium. This species is practically indifferent to section distribution and occurs through a wide range of pH values, though less frequently in the more acid groups (Table V).

Pleuronema. In the case of this animal the distribution through the sections is similar to that of *Paramoecium* except that there is a more definite falling off in the first and last sections. This is of interest in view of the fact that there is a narrower pH range in which *Pleuronema* occurs. As is seen from the table the optimum range lies between 6·5-7·6, and as the pH values outside this range tend to occur in the top and bottom sec-

tions the lower numbers of occurrences in these two situations are explained (Table VI).

Arcella. *Arcella* shows a very marked preference for the lower sections of the filter. In these sections (5 and 6) it occurs freely at all pH values; nevertheless in these two sections and still more in sections 1 and 2 there is definite evidence that it prefers an acid medium (Table VII).

Cinetochilum. *Cinetochilum* also shows a preference for the three lower sections; but in this case, although it can occur freely at pH values down to 6.1 greater degrees of acidity definitely act as limiting factors (Table VIII).

Bodo. This particular species shows a slight falling off in numbers at the bottom of the filter; but like *Trepomonas* it is not one of the commoner forms found. As regards its pH distribution it exhibits curious irregularities, for reference to the table demonstrates that maximum development occurs at an acid value of about 5.3 and again at an alkaline one of about 7.6. It is possible that this peculiarity was due to the presence of different physiological strains, but the evidence is insufficient to establish this with certainty (Table IX).

Effect of food supply. The effects of three changes in the composition of the solution to be filtered were studied, these changes being the omission of phosphate, the substitution of urea for ammonium sulphate, and of lactic acid for sucrose. The period during which phosphate was omitted was only a short one, 11 days: and though only tentative conclusions can be drawn from such limited data, it was thought worth while to present the results. Table X gives the percentage of occurrences of the different species during the period when the filter was receiving no phosphate compared with the previous 11 days when the population was receiving a normal diet. In general the omission of phosphate causes a reduction in numbers, but *Colpidium* and *Cinetochilum* are exceptions to this rule. The slight falling off of the other species is what might be expected owing to the lowering of the bacterial numbers and therefore the food supply; but this would only be a gradual effect as the filter for the first few days had reserves of phosphate. Why this effected *Colpidium* and *Cinetochilum* in the reverse manner is inexplicable.

The effect of urea (Table XI) was a depressing one on most species though again *Colpidium* was increased as was *Pleuronema*. These results are interesting, though difficult of explanation, since the expectation would be that urea would have no effect, for it normally breaks down to give salts of ammonia.

Another set of conditions connected with a change in the food supply arose when lactic acid was given to one filter instead of sucrose, the object being to study the effect of extreme acidity on the protozoan population. The average pH value of the effluent from the top section during the period when lactic acid was given was 4.0, but in all the other sections the effluents showed no increase in acidity above the normal values that were found when the filters were receiving sucrose. As is seen from Tables III-IX a pH value of less than 4.9 limits the occurrence of all the protozoan species under

Table III. *Trepomonas agilis. Effect of pH values.*

| pH range | Section 1 | | Section 2 | | Sections 5 and 6 | |
|-----------|--------------|--------------|--------------|--------------|------------------|--------------|
| | No. of cases | % occurrence | No. of cases | % occurrence | No. of cases | % occurrence |
| Under 4.9 | 27 | 0.0 | 8 | 25.0 | — | — |
| 4.9-5.2 | 5 | 40.0 | 5 | 60.0 | — | — |
| 5.3-5.6 | 17 | 41.1 | 17 | 58.7 | 16 | 33.3 |
| 5.7-6.0 | 36 | 41.7 | 39 | 46.1 | 2 | 50.0 |
| 6.1-6.4 | 23 | 52.3 | 36 | 47.2 | 21 | 14.2 |
| 6.5-6.8 | 70 | 62.0 | 115 | 40.0 | 59 | 8.4 |
| 6.9-7.2 | 38 | 55.1 | 66 | 39.4 | 146 | 18.5 |
| 7.3-7.6 | 10 | 30.0 | 14 | 21.4 | 72 | 15.3 |
| Over 7.6 | 5 | 40.0 | 8 | 37.5 | 22 | 27.1 |

Table IV. *Colpidium colpoda. Effect of pH values.*

| pH range | Section 1 | | Section 2 | | Sections 5 and 6 | |
|-----------|--------------|--------------|--------------|--------------|------------------|--------------|
| | No. of cases | % occurrence | No. of cases | % occurrence | No. of cases | % occurrence |
| Under 4.9 | 36 | 38.9 | 8 | 50.0 | — | — |
| 4.9-5.2 | 10 | 50.0 | 6 | 50.0 | — | — |
| 5.3-5.6 | 72 | 68.1 | 21 | 47.6 | 6 | 50.0 |
| 5.7-6.0 | 34 | 67.6 | 30 | 83.3 | 3 | 66.6 |
| 6.1-6.4 | 25 | 84.0 | 34 | 73.5 | 21 | 81.1 |
| 6.5-6.8 | 86 | 86.1 | 112 | 58.1 | 66 | 19.7 |
| 6.9-7.2 | 40 | 90.0 | 70 | 72.8 | 150 | 48.0 |
| 7.3-7.6 | 13 | 69.3 | 14 | 100.0 | 71 | 26.7 |
| Over 7.6 | 5 | 100.0 | 8 | 100.0 | 22 | 68.2 |

Table V. *Paramoecium putrinum. Effect of pH values.*

| pH range | Section 1 | | Section 2 | | Sections 5 and 6 | |
|-----------|--------------|--------------|--------------|--------------|------------------|--------------|
| | No. of cases | % occurrence | No. of cases | % occurrence | No. of cases | % occurrence |
| Under 4.9 | 36 | 25.0 | 8 | 37.5 | — | — |
| 4.9-5.2 | 12 | 33.3 | 6 | 66.6 | — | — |
| 5.3-5.6 | 29 | 41.8 | 19 | 26.3 | 6 | 33.3 |
| 5.7-6.0 | 38 | 50.0 | 40 | 57.5 | 3 | 100.0 |
| 6.1-6.4 | 26 | 61.6 | 33 | 75.8 | 21 | 28.5 |
| 6.5-6.8 | 90 | 83.3 | 111 | 81.1 | 64 | 65.5 |
| 6.9-7.2 | 52 | 82.7 | 63 | 68.3 | 147 | 74.4 |
| 7.3-7.6 | 12 | 66.7 | 14 | 71.5 | 71 | 63.4 |
| Over 7.6 | 5 | 80.0 | 8 | 75.0 | 22 | 63.1 |

Table VI. *Pleuronema chrysalis. Effect of pH values.*

| pH range | Section 1 | | Section 2 | | Sections 5 and 6 | |
|-----------|--------------|--------------|--------------|--------------|------------------|--------------|
| | No. of cases | % occurrence | No. of cases | % occurrence | No. of cases | % occurrence |
| Under 4.9 | 32 | 0 | 8 | 12.5 | — | — |
| 4.9-5.2 | 12 | 8.5 | 6 | 0 | — | — |
| 5.3-5.6 | 27 | 25.9 | 19 | 5.2 | 6 | 0 |
| 5.7-6.0 | 39 | 20.5 | 40 | 32.5 | 3 | 0 |
| 6.1-6.4 | 30 | 53.3 | 34 | 47.1 | 21 | 23.9 |
| 6.5-6.8 | 98 | 77.5 | 112 | 78.6 | 65 | 23.1 |
| 6.9-7.2 | 52 | 88.0 | 68 | 66.2 | 149 | 55.0 |
| 7.3-7.6 | 10 | 50.0 | 14 | 100.0 | 70 | 61.4 |
| Over 7.6 | 5 | 60.0 | 8 | 25.0 | 22 | 18.1 |

Table VII. *Arcella vulgaris*. Effect of pH values.

| pH range | Section 1 | | Section 2 | | Sections 5 and 6 | |
|-----------|--------------|--------------|--------------|--------------|------------------|--------------|
| | No. of cases | % occurrence | No. of cases | % occurrence | No. of cases | % occurrence |
| Under 4·9 | 1 | 0 | 2 | 100·0 | — | — |
| 4·9-5·2 | 3 | 33·3 | 1 | 0 | — | — |
| 5·3-5·6 | 13 | 15·4 | 17 | 23·5 | 2 | 100·0 |
| 5·7-6·0 | 32 | 9·4 | 29 | 31·1 | 7 | 100·0 |
| 6·1-6·4 | 36 | 13·9 | 29 | 34·5 | 33 | 89·9 |
| 6·5-6·8 | 41 | 9·7 | 52 | 7·7 | 98 | 68·4 |
| 6·9-7·2 | 62 | 14·5 | 52 | 9·6 | 168 | 71·5 |
| 7·3-7·6 | 2 | 0 | 3 | 0 | 13 | 69·3 |
| Over 7·6 | 0 | 0 | 0 | 0 | 0 | 0 |

Table VIII. *Cinetochilum margaritaceum*. Effect of pH values.

| pH range | Section 1 | | Section 2 | | Sections 5 and 6 | |
|-----------|--------------|--------------|--------------|--------------|------------------|--------------|
| | No. of cases | % occurrence | No. of cases | % occurrence | No. of cases | % occurrence |
| Under 4·9 | 2 | 0 | 4 | 0 | — | — |
| 4·9-5·2 | 2 | 0 | 3 | 0 | — | — |
| 5·3-5·6 | 15 | 0 | 17 | 5·9 | 2 | 0 |
| 5·7-6·0 | 32 | 9·4 | 32 | 21·8 | 7 | 28·5 |
| 6·1-6·4 | 34 | 23·5 | 31 | 35·5 | 34 | 55·8 |
| 6·5-6·8 | 43 | 27·9 | 45 | 22·2 | 98 | 70·5 |
| 6·9-7·2 | 34 | 29·4 | 42 | 28·6 | 136 | 65·5 |
| 7·3-7·6 | 0 | 0 | 3 | 33·3 | 4 | 50·0 |
| Over 7·6 | 0 | 0 | 0 | 0 | 0 | 0 |

Table IX. *Bodo saltans*. Effect of pH values.

| pH range | Section 1 | | Section 2 | | Sections 5 and 6 | |
|-----------|--------------|--------------|--------------|--------------|------------------|--------------|
| | No. of cases | % occurrence | No. of cases | % occurrence | No. of cases | % occurrence |
| Under 4·9 | 36 | 5·5 | 8 | 25·0 | — | — |
| 4·9-5·2 | 11 | 54·5 | 5 | 20·0 | — | — |
| 5·3-5·6 | 25 | 56·0 | 20 | 60·0 | 16 | 33·3 |
| 5·7-6·0 | 29 | 27·6 | 38 | 65·8 | 3 | 33·3 |
| 6·1-6·4 | 23 | 43·5 | 39 | 43·5 | 21 | 28·5 |
| 6·5-6·8 | 72 | 52·8 | 121 | 30·6 | 66 | 27·2 |
| 6·9-7·2 | 43 | 74·4 | 73 | 28·8 | 149 | 24·8 |
| 7·3-7·6 | 9 | 55·5 | 14 | 21·4 | 62 | 32·2 |
| Over 7·6 | 5 | 80·0 | 8 | 75·0 | 22 | 91·0 |

Table X. Effect of the omission of phosphate.

| Species | Total No. of observations, Sections 1-5 | Percentage occurrences | |
|--------------|---|------------------------|--------------|
| | | Normal diet | No phosphate |
| Colpidium | 55 | 19·8 | 73·3 |
| Paramoecium | 55 | 61·2 | 48·6 |
| Cinetochilum | 55 | 45·0 | 59·4 |
| Pleuronema | 55 | 50·4 | 43·2 |
| Bodo | 55 | 52·2 | 14·4 |
| Arcella | 55 | 50·4 | 32·4 |
| Trepomonas | 55 | 41·4 | 28·8 |

Table XI. *Effect of urea.*

| Species | Total No. of observations. Sections 1-6 | Percentage occurrences | |
|--------------|--|------------------------|------|
| | | No urea | Urea |
| Colpidium | 148 | 19.4 | 25.5 |
| Paramoecium | 148 | 79.8 | 63.0 |
| Cinetochilum | 148 | 51.6 | 42.9 |
| Pleuronema | 148 | 54.9 | 74.4 |
| Arcella | 148 | 57.0 | 40.9 |

Table XII. *Effect of lactic acid.*

| Species | Total No. of observations | Percentage occurrences | | | | | | | | | | | |
|-------------|---------------------------------|----------------------------|-------|---|------|------|---|---------------------|---|------|---------------------------|---|---|
| | | Before lactic. Sections | | | | | | Lactic. Sections | | | After lactic. Sections | | |
| | | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 |
| Bodo | 36 | 39.2 | 8.4 | | 5.6 | 2.8 | | 0 | | 5.6 | | | |
| Trepomonas | 36 | 58.3 | 2.8 | | 25.2 | 2.8 | | 14.0 | | 0 | | | |
| Colpidium | 36 | 81.2 | 25.2 | | 0 | 0 | | 2.8 | | 0 | | | |
| Paramoecium | 36 | 98.0 | 100.0 | | 70.0 | 98.0 | | 100.0 | | 75.5 | | | |
| Pleuronema | 36 | 95.2 | 42.0 | | 33.6 | 22.4 | | 92.4 | | 11.2 | | | |
| Lionotus | 36 | 30.8 | 84.0 | | 2.8 | 5.6 | | 47.5 | | 2.8 | | | |

consideration to some extent, therefore as might be expected the top section during the lactic acid period was almost devoid of living Protozoa, though bacteria and fungi were present and good purification was ultimately obtained. The fact that the percentage purification brought about by the top section changed from 17 on the second day of the experiment to 58 on the fourteenth day suggests that the bacterial population also underwent a marked change, strains presumably being selected out from the normal population which were able to oxidise the acid, while the development of the sucrose splitting strains was inhibited. Table XII shows the percentage occurrences of each species in the top and bottom parts of the filter during the lactic acid period, when observations were made during 12 days, and also during the 12 days immediately preceding and following this period when the food supply was normal. It will be seen that *Paramoecium* shows no change in numbers except in the top half of the filter during the acid period, the diminution being entirely due to the absence of this organism from the top section (average pH 4.0). *Pleuronema* was depressed throughout the acid period but recovered as soon as normal food was resumed; the other four species considered not only were very much reduced during the acid period, but showed little or no recovery in the succeeding period, except in the case of *Lionotus* when there was a definite rise in numbers. In the case of the other species no recovery took place, and they were not seen until the gravel of the filter had been autoclaved and reinoculated. Reinoculation of the sections before sterilisation had no effect. These results suggest that in these species it is the flora encouraged by the lactic acid that is imimical, while in the case of *Pleuronema* and still more in that of *Lionotus* it is possibly the oxidation products of the acid that inhibit development.

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V. SUMMARY.

1. The purity of a medium, as measured by the amount of reducing material present in the solution, and the food supply, are two of the principal factors influencing the distribution of Protozoa in sewage filters.
2. The Protozoa considered occur throughout a wide range of pH values, but the optima for different species are different.
3. Where chemical compounds added to the solution affect the protozoan population adversely, it may be due either to the formation of deleterious oxidation products, or to the development of a bacterial flora which is inimical to the Protozoa.

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CLIMATE IN CAVES AND SIMILAR PLACES IN PALESTINE

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I. INTRODUCTION.

It is well known that great differences exist between the climate studied by meteorologists under standard conditions, and that which prevails in the actual places where plants and animals live. It is the purpose of this paper to record some observations made in Palestine on temperature and humidity in caves and small cavities in rocks, during the height of the dry summer.

The climate of Palestine is essentially Mediterranean. The rainfall is not inadequate in amount, but it is very irregularly distributed throughout the year: the greater part of the rain in all parts of the country falls in a few winter months: the total rainfall also varies very widely between one year and the next. The temperature in winter is so low that the rain is of little importance to the plants and animals. The spring is the only time of the year when the greater part of the living things are fully active. The soil is still wet: a little rain may fall: and the temperature has begun to rise. But from May until the first heavy rain, which is expected in November, the climate is dry, bright and windy. Evaporation is therefore very intense; the soil for the most part is bare and the plants and animals appear to have ceased to exist. But though the country appears to be so dry, one wonders whether the winter rain is still of value to the flora and fauna: is there much or little moisture in the soil at a depth of a foot or two? Is water evaporating from the soil into the atmosphere? Can we demonstrate that evaporation is moistening the air in a cave, or a crack in a rock?

The insect fauna of Palestine has been collected fairly efficiently, but we have little knowledge of the biology of most of the species. With few exceptions, we do not know where they pass the summer, or at what stage they do so. As it is impossible to find them by ordinary methods, and as there is little for them to eat on the surface of the ground, we must assume some of them may be feeding on roots but that most of them are dormant in some stage of their life history. I visited Palestine in June and July, 1931, for the purpose of exploring certain environments and of making use of methods of hygrometry. The present paper deals with observations made in the caves during the summer, also in small cracks in rock and in cavities in rough walls. I have published elsewhere (2) a discussion of some data which I collected in rat-holes and of the relation between the climate in those places and the biology of fleas. At the time of my visit the rain had been slight and

irregular since the first week in March: the total rainfall from March 8th till June had been 16 mm. in Jerusalem.

II. METHODS.

In a cave, atmospheric temperature and humidity may be studied by standard meteorological methods. The most convenient apparatus to use is the whirling psychrometer, which gives readings of the dry and wet bulb. These are converted by the Assmann tables to give readings of humidity on any scale which is desired. The temperature and humidity in a crack in a rock, or a small cavity in a loosely built wall, are much more difficult to measure. I tied a very short (4 in. = 10 cm.) mercury thermometer to a piece of stout wire, and was able to push it two or three feet into these places. Humidity was measured by pushing a piece of thick-walled rubber tubing into the cavity, and aspirating a sample of air into an enclosed dew-point apparatus. The data having been collected, I converted the humidity readings to three scales. I used "relative humidity" because it is the most familiar and because it is frequently quoted in meteorological publications. But for many purposes one requires "vapour pressure": for instance, if it is shown that the vapour pressure is consistently higher in a cave than it is outside, that is evidence that water is evaporating from the rock into the cave: it is also evidence that water will diffuse out of the cave into the external atmosphere. But for biological purposes, it is now known that the best measure of humidity is "saturation deficiency." It has recently been shown (1), that the loss of water from insects probably follows this law: it is at any rate known that it is more nearly proportional to saturation deficiency than it is to any other measure of humidity.

It may be asked to what extent measurements taken at particular moments are of value in indicating the climate throughout the 24 hours. From observations made elsewhere in the soil and in caves¹, we are justified in saying that the diurnal range of temperature in these situations is very slight and frequently immeasurable. Assuming that evaporation into the cave will be at a steady rate throughout the 24 hours, one may say that observations on temperature and humidity taken at any one moment give a very fair indication of the climate prevailing throughout the 24 hours. But the superficial layers of the soil are not at a steady temperature, particularly in such a country as Palestine where the earth is bare of vegetation and exposed to intense solar radiation: the facts collected from cracks in a wall should therefore be accepted with caution.

¹ For a general review of soil temperature and the theory of the flow of heat through soil, see 5. For soil temperatures under climatic conditions similar to those prevailing in Palestine, see 4, 6, 7, 8. For soil temperatures and cave climates see 9, (10, (11).

III. THE CAVE CLIMATE.

The greater part of Palestine consists of limestone, which occurs in hard and soft strata. It contains a very large number of caves, some of them excavated entirely by water, others artificial: some of the artificial ones are of great extent and complexity. Some have originally been quarries, others cisterns, others strongholds: the earliest date from remote periods in the early Stone Age: the most recent were excavated during the Great War. There are all sizes, the smallest being not more than a few yards across. In the course of the investigation I made a study of nine small caves (less than 100 ft. (30 m.) in their greatest dimension), also of eight large caves. In each of them I took readings, generally in several places, with a whirling psychrometer: a selection of the readings and of the values that may be reduced from them is given in Table I. No correction has been made for barometric pressure. In each cave I also made a search for animals and particularly insects, looking over the walls with an electric light and also turning over stones on the floor.

Among the smaller caves three have been selected, and the data appear in Table I. The first was on the floor of the Wadi Hamam, Galilee. The mouth of the cave is about 15 ft. by 8 ft. (4·5 m. by 2·4 m.): the floor is about 120 ft. (36 m.) in each direction, and the height 20 ft. (6 m.). The floor had clearly been wet in the winter but was dry at the time of my visit. The readings show that there was almost no difference in vapour pressure between the atmosphere in the cave and that outside. The saturation deficiency was less in the cave, depending directly on temperature. Here then we have a simple case in which the relative humidity is dependent on temperature and not complicated by local evaporation. The cave at Bethany was an extremely shallow excavation in the chalk by the side of the road. The mouth was 10 ft. wide by 3 ft. (3 m. by 1 m.) high; from back to front the cave measured only 10 ft. (3 m.). A strong wind was blowing across the mouth of it, but in spite of that and of the freedom of diffusion from so small a cave, the vapour pressure was materially greater inside, showing that active evaporation from the rock into the atmosphere was taking place. The climate in this cave is therefore more complex than in that of the Wadi Hamam because of the evaporation. The cistern which appears in the table is close to the English cathedral in Jerusalem. It has been cut into the side of a hill so that it is completely closed above by unaltered rock, but it has a large opening at the side by which one may pass into it. The surface of the water (*B*) at which the readings were taken is only 6 ft. (1·8 m.) from the place outside (*A*), and *B* is exposed to broad daylight. One would suppose, therefore, that diffusion would be so free that the humidity inside would hardly exceed that outside, but the facts quoted in the table show that this is far from being the case. Evaporation from the surface of the water was active enough to raise the absolute humidity very greatly.

Table I. *Conditions of temperature and humidity in caves. Readings of dry and wet bulbs, obtained with a whirling psychrometer; other values reduced from them by Assmann tables. Under "time" is given the hour, day and month; thus 18, 15th VII means 6.0 p.m. on July 15th. In each case A signifies readings taken in open air; B, C, etc. those taken inside the cave.*

| Place | Time | Whirling psychrom. | | Rel. hum. % | Vap. press. mm. | Sat. def. mm. |
|-------------|----------------|--------------------|------|-------------------|-----------------------|---------------------|
| | | Dry | Wet | | | |
| W. Hamam | 11, 8th VI | 28.0 | 22.5 | 62 | 17.7 | 10.7 |
| | " B | 24.0 | 21.5 | 80 | 18.0 | 4.4 |
| Bethany | A 18, 15th VII | 27.8 | 18.2 | 39 | 10.9 | 17.1 |
| | " B | 27.4 | 18.8 | 44 | 12.0 | 15.4 |
| Cistern | A 18, 16th VI | 25.4 | 14.2 | 27 | 6.5 | 17.8 |
| | " B | 23.0 | 17.4 | 58 | 12.1 | 9.0 |
| Jenin | A 12, 7th VI | 27.5 | 20.5 | 53 | 14.6 | 13.0 |
| | " B | 23.5 | 20.5 | 76 | 16.6 | 5.1 |
| " | C " | 21.5 | 20.0 | 87 | 16.8 | 2.4 |
| | " D | 20.0 | 20.0 | 100 | 17.5 | 0.0 |
| Beit Jabrin | A 14, 20th VI | 31.4 | 20.0 | 34 | 11.8 | 22.6 |
| | " B | 21.0 | 17.6 | 72 | 13.4 | 5.3 |
| | " C | 18.0 | 17.8 | 98 | 15.2 | 0.3 |

The atmosphere in several of the smaller caves contains much more water than the surrounding air: one would therefore expect to find the air saturated, or nearly so, in the larger caves, because the distance from the exterior is greater so that diffusion is less free. This was the case in most of the caves examined. An artificial tunnel close to the road a mile or two south of Jenin may be taken as an example. The entrance is about 5 ft. by 10 ft. (1.5 m. by 3 m.); 24 ft. (7.2 m.) from the mouth (*B*) one is still in broad daylight, and passes a well in the floor which contains frogs and aquatic insect larvae. The passage then narrows and one has to crawl about 20 ft. (6 m.). At this point, at which one can stand, the cave branches; readings (*C*) were taken here. Neglecting the branch of the cave which passes upwards on the left, it is possible to walk a further 20 ft. (6 m.) and then to mount steeply to a point 60 ft. (18 m.) further, where the cave is blocked by a fall of rock. Readings (*D*) were taken here. A study of the figures which are given in the table shows that the further one penetrated, the nearer the air approached to saturation. It was completely saturated at the end. The fact that the tunnel was much narrowed at one point, no doubt reduced diffusion and tended to raise the atmospheric moisture in the more remote parts. Similar observations were made in several other large caves, for instance the Tombs of the Kings and King Solomon's Quarries at Jerusalem, and the large cave known as Mugharet el Wad on the western side of Mount Carmel. In all of these the atmosphere in the deeper parts of the cave was saturated with moisture, and in the last two water was dripping from the roof in several places. In all these wet caves there is a deep layer of soil and chalk above the roof, and it is clear that this holds enough of the winter rain to saturate the atmosphere of the cave even in the middle of the dry summer.

I was able to work in one cave in which the layer of soil and rock above the roof was only about 10 or 15 ft. (3–5 m.). This was the so-called Phoenician cave at Beit Jabrin. It is cut in soft limestone in the side of a low mound, and it consists of several chambers the sides of which are lined with niches in which bodies were buried. The readings (*B*) were taken in a niche at the end of the first chamber only 30 ft. (9 m.) from the door. Beyond that point one crawled 6 ft. (2 m.) and then stood in a second chamber. At this point one was perhaps not more than 40 ft. (12 m.) from the door, but the passage twisted and was obstructed. The readings taken here (*C*) show that the air was very nearly saturated. This is surely remarkable, for the roof of the cave was a comparatively shallow layer of material which one would have supposed was entirely dry.

IV. THE INSECT FAUNA OF CAVES.

The fact that I have previously lived in Palestine made me familiar with the animals and with the special problem of collecting. In June and July one can find hardly any insects on the surface. In the evening, a few insects which cannot be collected at midday are visible; but even then one may walk several hundred yards and see nothing but a few grasshoppers and Tenebrionid beetles. One might suppose that many insects would be discovered aestivating in the caves, particularly as the saturation deficiency in them is so little and presumably so constant; but in fact I was able to discover very few. The special object of my search was the mosquito, *Anopheles sergenti*, a species which is common in Palestine in the autumn, but extremely rare all through the hot weather. I had hoped that I might discover adults aestivating, but none were found in any of the caves explored. In all the caves visited the only mosquito was a single male *Theoboldia longiareolata*. Other Diptera were adults of *Phlebotomus*, which were frequently seen, and a few Muscidae of several species in the cave south of Jenin. In nearly all the caves, both large and small, one found very large numbers of adults of *Medetera dendrobaena* (Dolichopodidae) (det. Parent). Of the Lepidoptera a very few Noctuidae were found, particularly in shallow caves running only a few yards into the limestone. Tineina were more frequent, and Mr E. Meyrick has identified three species. *Tinea fuscipunctella* was taken in the cave south of Jenin, and *Oegoconia quadripunctata* in several artificial caves in and about Jerusalem. Both these species appear to breed in excrement or dry vegetable refuse, and it may be assumed that they are actual natives of the caves. In the cave at Mugharet el Wad I found a large number of *Acrolepia granitella*. This species feeds in mines in the leaves of *Inula dysenterica*, and presumably the adults had wandered into the cave from the exterior. There is a previous record (3) of this insect being found in a cave: in a cave near Lourdes, at about 50 ft. (15 m.) from the outside, large numbers of individuals were found sitting on the wall of the passage which leads to the cavern. In the dust on

the floors of some of the caves, particularly one in the Wadi Hamam inhabited by pigeons and swifts, I found nymphs of a cockroach (*Polyphaga*). From these scanty records one can conclude that, whatever else the insects do, they do not aestivate in caves.

V. CLIMATES IN CAVITIES IN WALLS.

The facts collected in the caves demonstrate that, even in summer, enough evaporation is taking place to raise the absolute humidity. Presumably therefore the general surface of the soil is losing moisture, though this would be difficult to demonstrate because the water vapour is so rapidly mixed in the atmosphere by diffusion and wind. But it might be possible, by using appropriate methods, to demonstrate that the absolute humidity is higher in a crack in a rock, or a cavity in a wall, than it is outside.

The facts published in Table II were collected in a garden in Jerusalem, on ten occasions between 8 a.m. and 6 p.m., July 15th–23rd. In the garden there was a wall, which faced north and supported a terrace of soil. It was roughly built of large irregular fragments of rock, fitted together but not cemented. It was possible to introduce lengths of thick-walled rubber tubing into the interstices of the wall, and to withdraw samples of air from positions about 18 in. (45 cm.) from the face of the wall. I introduced three rubber tubes, 8, 20 and 34 in. (20, 50 and 85 cm.) from ground level, and left them permanently in position during the investigation. The hygrometry of the samples of air withdrawn was by dew-point.

Table II. *Conditions of temperature and humidity in the open air of a garden, and at three levels above ground, in a terrace wall. Data are based on ten sets of readings, taken in mid July, between 8 and 18 hours. Humidity is given as relative (R.H.), absolute (V.P. in mm. Hg), and saturation deficiency (Sat. def.).*

| | Outside | | | | At 8 in. (20 cm.) | | | |
|--------------------|--------------|-----------|-------------|--------------------|-------------------|-----------|-------------|------------------|
| | Temp. °C. | R.H. % | V.P. mm. | Sat. def. mm. | Temp. °C. | R.H. % | V.P. mm. | Sat. def. mm. |
| Mean | 26.76 | 51.8 | 13.42 | 13.37 | 24.35 | 64.6 | 14.77 | 8.19 |
| Maximum | 30.0 | 73 | 14.8 | 21.2 | 27.0 | 78 | 16.0 | 10.8 |
| Minimum | 22.4 | 37 | 11.1 | 5.5 | 22.0 | 60 | 12.8 | 4.4 |
| At 20 in. (50 cm.) | | | | At 34 in. (85 cm.) | | | | |
| | Temp. °C. | R.H. % | V.P. mm. | Sat. def. mm. | Temp. °C. | R.H. % | V.P. mm. | Sat. def. mm. |
| Mean | 24.60 | 59.9 | 13.80 | 9.52 | 25.45 | 55.8 | 13.50 | 11.04 |
| Maximum | 27.0 | 76 | 15.5 | 12.8 | 28.0 | 73 | 15.0 | 15.1 |
| Minimum | 22.0 | 49 | 10.9 | 4.9 | 22.5 | 45 | 11.6 | 5.4 |

The following points in Table II call for comment. The differences in temperature are of no significance because the range of temperature is doubtless different in each position, and so is the time of day at which maximum or minimum occurs. The temperature readings are necessary in order to obtain the relative humidity and saturation deficiency from the dew-point reading.

It will be observed that the absolute humidity (v.p.) is consistently higher in the wall than outside, and that it is higher near the foot of the wall than near the top. The saturation deficiency is clearly less in the wall, especially at 8 in. (20 cm.) from its base, than it is outside. This appears in the mean figures, and also in the maxima and minima. The saturation deficiency is dependent on temperature and will therefore be different at different times of day and night. But the values of saturation deficiency have this particular interest, that they were recorded during the hours when the temperature (and therefore the saturation deficiency) outside the wall is highest. The figures show that at this time of day, when loss of water from organisms is most rapid, conditions are materially less unfavourable in the wall.

A number of isolated readings were taken in cracks in rocks in several places in Palestine. They support the general conclusion that, even if a sample is drawn from a point within 2 ft. of the surface of the rock, its absolute humidity is much higher than that of the air outside.

VI. FAUNA OF CAVITIES IN WALLS, ETC.

No thorough study of the fauna was possible in the time available. If one were able, it would be interesting to demolish one of these walls, and investigate the creatures, passing the débris through sieves. In the course of collecting the climatic data I frequently found Isopods and large millipedes in the walls, and observed that before sunset both these creatures came out and wandered over the surface of the ground. Adult *Phlebotomus* were occasionally dislodged.

VII. CONCLUSIONS.

It is shown that, in most of the caves and cavities which were investigated, evaporation from the soil into the atmosphere was going on, in June and July. This is interesting in view of the fact that very little rain had fallen for several months previously. It is remarkable that, even if the sampling tube can only penetrate a foot or two from the surface of a rough wall, it reaches an atmosphere in which the absolute humidity is higher than it is outside. The differences in saturation deficiency which were observed between the air in the spaces in the wall and that outside are sufficient to be of considerable biological importance.

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CONCERNING FLUCTUATIONS IN MARINE FOOD FISHES

By B. STORROW, M.Sc., A.L.S.

(*With one Figure in the Text.*)

THERE appear to be three fundamental axioms in connection with fluctuations in fisheries—fish are hatched, fish can swim, and fish die¹.

When there is a good year for hatching and development we get what is called a good year-class, as that arising in the Norwegian herring fishery for 1904, the southern North Sea herring fishery for 1922 and in the Tyne salmon fishery for 1923. Exactly what causes the production of a good year-class we are far from sure. We try to think in terms of what we imagine are suitable conditions for the young and chiefly about all the factors, physical and chemical, likely to give an abundance of food at the proper time; but rarely do we concern ourselves with the quality of the eggs from which the young are hatched or the adults producing them.

The swimming of fish varies with season and maturity and, when regular, gives rise to well-established fisheries. Migrations vary with age also, from the passive drift of the young to the active and often very extensive movements of the adults which may show variation with age also, even after first maturity. These movements are associated with currents, and it is this association which has attracted my attention a great deal when suggesting explanations for fluctuations in post-war years in terms of changed migrations.

It is changes in migrations which give rise, probably, to some of our difficulties in estimating the value of year-classes. In some herring fisheries the young fish fail to join the commercial shoals, or appear not to do so, and there have been cases of a year-class reappearing after its numbers suggested it was no longer of much value. Similar change in migrations may take place amongst the cod supplying the Lofoten fishery, for the evidence as to catches and quantities of liver and roe suggests that the differences recorded may not be due altogether to young fish joining the shoals. With change in migrations there is redistribution and the fish of one area are caught many miles away. The original grounds may then show a failure and the new grounds may, or may not, give increased catches, depending on the extent to which the migrants replace or are assimilated by the fish of that area. Changes benefiting one area at the expense of another have been termed sympathetic fluctuations. The failure of the North Sea herring fishery of 1921 appears to have been due, in part at least, to an extended migration of fish at or near

¹ For a summary of recent research on marine fishery ecology, with references to literature, see **E. S. Russell** (1932), *Journal of Ecology*, 20, 128.

the end of their third year and when approaching first maturity. The evidence is based on the marked scales of the herrings caught off the north of Scotland in 1923, their calculated growth for the first three years being such as found in the North Sea, while that for 1921 and 1922 was of an oceanic type. The sudden increase of cod in Davis Strait, the exceptional catches made on Bear Island grounds in recent years and the cod fishery of Spitsbergen in the late 'seventies and early 'eighties of last century were all due, probably, to change in migrations, and they serve to indicate the difficulty of estimating the value of year-classes. In connection with the herring there is still further difficulty, at least for some grounds, owing to fish moving to waters further from the coast with increasing age, as shown by samples taken along the north coast of Scotland and about the Shetlands.

With regard to mortality we are inclined to think solely in terms of man's actions. It is not often that mortality on a large scale and due to natural causes has affected fisheries, but there have been cases. The enormous haddock mortality of 1789 to the north-east of the North Cape was followed by exceptional scarcity on our north-east coast; wholesale destruction preceded the disappearance of the fishery for tilefish in American waters in 1882; and there have been several cases of serious and sudden death-rates off the South African coast. The mortality due to the action of man may be estimated only when we are fairly sure that migrations with age do not bring about decrease in the older fish on the grounds and when no violent fluctuations occur. In the case of fisheries in narrow waters and for fish performing small migrations there is some hope for success, but with open and oceanic waters and fish making great migrations the estimation of mortality becomes impossible. The number of herrings with marked scales, found about the north of Scotland since 1923 and taken as indicating change in growth due to migrations, suggest difficulty in estimating the mortality of a pelagic fish in a comparatively small area such as the North Sea. No possible clue can be obtained under present conditions as to the rate of mortality in the shoals of oceanic herrings, giving or adding to our winter fisheries from north-west Ireland to the Shetlands; for the year-classes of cod yielding catches from new and northern grounds; and none could have been obtained for the American mackerel during last century, when great and violent fluctuations occurred, even if it had been possible to ascertain its age. As a general rule we agree that man is unable to destroy a species completely and that he can reduce the size of the fish in certain areas, but we differ considerably as to the necessity for restrictions and may base our objections to legislation on our ignorance of natural fluctuations.

At one extreme of our problem are the factors which produce atmospheric and oceanic circulation and at the other the physiological complexities demanding the minutiae of chemical knowledge and technique and producing psychological intricacies. For the purpose of fluctuations in food fishes and

for measuring these fluctuations it is not sufficient for us to know that catches, migrations and reproduction may vary with salinity, temperature and the mixing of waters. We require information as to what amount of change in environment is necessary to bring about change in the fish and, if possible, a measure is desirable. Also, we wish for as many details as possible as to the cause of change in waters.

Most of us, at one time or another, have joined in the search for periodicities, and we will continue to do so whilst we work at fluctuations. Periodicities have a strange attraction and one becomes addicted to them. Here we are looking for coincidences, but it would be extremely difficult at times to say exactly what we expect or why we expect it. We examine manifestations and think in terms of causes, and it is often more satisfactory to find a lag than to get complete coincidence. We find a double cusp in our curve for manifestations when there is a simple curve for assumed cause, and, in addition and with a simple curve for cause, we get an inequilateral curve for manifestations. Many of our difficulties arise from the fact that we are dealing with a minor cause acting during a period of greater change and our neglect of optimum conditions for the phenomenon concerned.

Recently I have obtained some evidence of a period of approximately 70 years in salmon fluctuations. The evidence cannot be considered quite satisfactory, nor can the evidence of greater change during a longer period. An attempt has been made to show such a period acting during greater change in the accompanying diagram (Fig. 1), in which imaginary optimum conditions are indicated also. The figure suggests how maxima and minima may occur at varying intervals, which of themselves alone would give little clue to the true periodicity of the cause acting.

To argue, without further data, that a period of 70 years was the prime cause of fluctuations in fisheries would be much more absurd than to state it was of solar origin because it consisted of twice 35 years. We are all familiar with the so-called 11-year period for solar activity as manifested by sunspots, which reach their maxima at much more irregular intervals than the term implies. A lunar period of about 90 years has been suggested as responsible for change by Otto Pettersson, who has drawn attention also to the influence of an 18 to 19-year period in fisheries and which may account for some evidence of change I have found recently in salmon fisheries during the past 150 years or so. This 18 to 19-year period is probably connected with the moon's nodes, and in addition we have a period of about 9 years, arising from the lunar apsides and not coinciding with the half of the 18 to 19-year nodal period. No one would state that the sun and moon are without some influence on the atmosphere and waters of the earth, and there is a possibility that each and every of these periods is concerned with fluctuations. We may be able to fix the duration of these periods, but we can make no approximation to their values, still less can they be referred to optimum conditions. It is

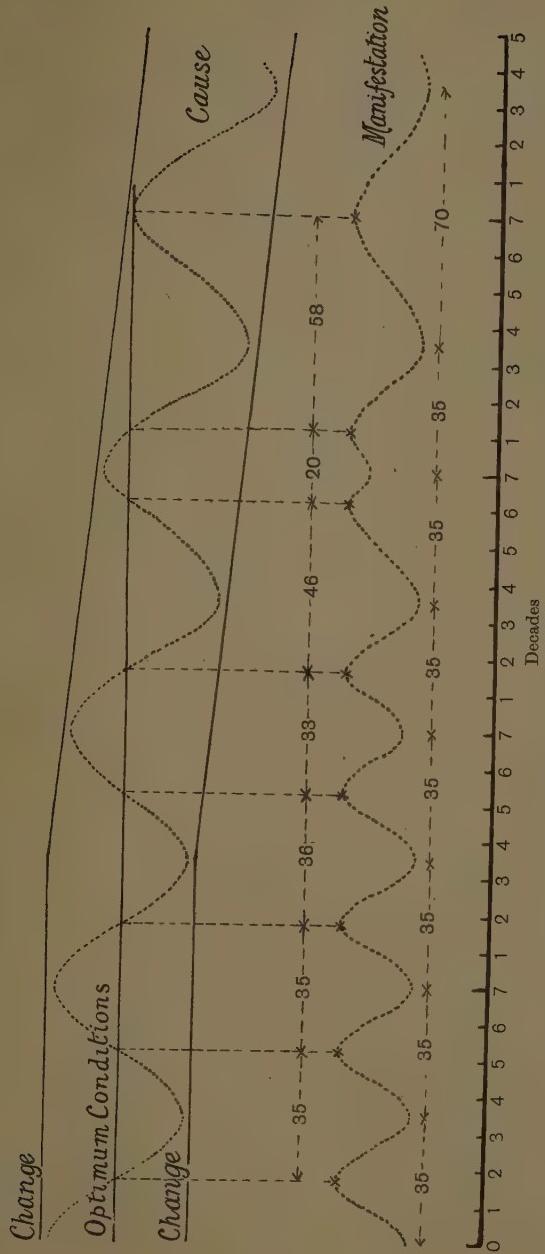


Fig. 1. The diagram illustrates a 70-year period in the environment acting during greater change, in reference to the optimum condition for a species, and the result on the numbers of the fish. (Hypothetical diagram.)

possible that they vary in importance, and the predominant cause of one period may be the secondary cause of another.

And what are optimum conditions? Our failure to rear any of the chief marine food fishes in quantity is a sure indication of our ignorance as to their numbers and values. We do not know if an understanding as to rearing would give the optima for adults, nor do we know whether they change during a period of greater change. If a creature be truly a victim of its environment it would be strange if optimum conditions are constant for all time.

The search for periodicities involves a consideration of mean conditions, and at once the question arises as to whether means have any stability or are simply a convenience. We are confronted with a multiplicity of data, and one of our greatest difficulties is the arranging of these in order to obtain suggestions from coincidences as to probable cause and effect. Departures must be recorded, but whether, at the present time, they should be referred to the mean over the available period or are better stated in a comparative way is not a matter for dogmatism.

Arising from coincidences and periodicities comes the temptation of prophecy, and to write of prophecy is to confess. The foretelling of the future of a well-established fishery is not easy even with a large number of coincidences to guide us, but to attempt to do so for a fishery in an intermediate region, between narrow waters and oceanic conditions and where catches may depend on at least two classes of fish—their presence, absence, or mixing—is to court disaster. Somewhere in my desk is a number of letters, if they have not been destroyed, and individually they confirm some prophecy attempted. They range from the herring fishery of north-west Ireland round the north of Scotland to East Anglia, and the successes include, amongst others, the condition of these fisheries, the return of shoals to the west of the Shetlands after an absence of about 19 years, and the production of the 1922 year-class. The winter fishery off the north-west of Ireland and the coming of a new year-class in 1924 had been successfully foretold, but the young fish were expected to have three winter rings and they had four. It was the inability to account for this difference in age which caused me to realise that my mental condition was equal to the physical condition of some of the prophets of old. The value of prophecy as an aid to fluctuations depends entirely on our mental attitude. No better way is known for obtaining clues to contributory causes, and anyone bold enough to state his views openly as to the future of any fishery deserves our charity.

There is great difficulty in placing marine food fishes under observation in their natural surroundings. Temperature, salinity, aeration and *pH* values in tanks may show no difference from sea conditions and it is a comparatively easy matter to keep many of them alive. But space and food seem to be associated, for overfeeding in a restricted space and where swimming is limited is followed by death. Cod, whiting, plaice and other flat fish will

spawn and give progeny provided they are captured when of a fair size, but recently we have had some peculiar experiences in our tanks at Cullercoats. In 1923 young herrings, undergoing or just completing their metamorphosis, were caught in the bay and placed in our tanks. They were fed regularly on an artificial plankton comprised of mussels and shore crab chiefly, and they grew and lived, but showed abnormality in their tail fins, one or other of the lobes partly disappearing. Many of them lived until 1931 and during the time abnormalities appeared in some of their heads. They never showed any sign of sexual development and the gonads were in a virgin condition when examined. Growth after the second year was slow and winter rings were so poorly marked that age determination was impossible. In the same year, 1923, young plaice, the metamorphosis completed, were taken from shore pools and have lived in our tanks till now, April 1932; they show no signs of sexual development. The behaviour of these fish may be due to some food deficiency, probably a lack of calcium, but the fact remains that they did not develop sexually and we can only guess at the reason.

SUMMARY.

The importance of fluctuations in marine fisheries is pointed out and certain gaps in our present knowledge emphasised. The relation of periodicities in controlling environmental factors to the optimum conditions for fish is discussed.

THE GREY SQUIRREL (*SCIURUS CAROLINENSIS*) IN THE BRITISH ISLES, 1930-1932

By A. D. MIDDLETON.

(Bureau of Animal Population, Department of Zoology and Comparative
Anatomy, University Museum, Oxford.)

(With one Map.)

DURING the past two years grey squirrels have decreased greatly throughout the British Isles. Over most of their established range the numbers increased during 1928, 1929 and 1930 to a very high density in the summer and autumn of 1930¹. During the autumn, winter and spring, 1930-1, grey squirrels became greatly reduced in numbers in practically all districts where they had been numerous, sick and dead individuals being seen in many instances. Disease was recorded in comparatively few localities (notably at Ashridge Park, Hertfordshire, Stowe, Buckinghamshire, North Northamptonshire, and North Oxfordshire), but other observers reported a definite decline in the numbers for which no explanation other than the occurrence of disease could be given. On most country estates these squirrels had been persistently shot and trapped for several years, in spite of which they had continued to increase up to 1930, and it is generally admitted that the decrease during 1930-1 could not be solely attributed to killing by man. Grey squirrels became remarkably scarce at the same time in urban districts, public parks, and agricultural areas where little action had been taken against them: for example, in Regent's Park, London.

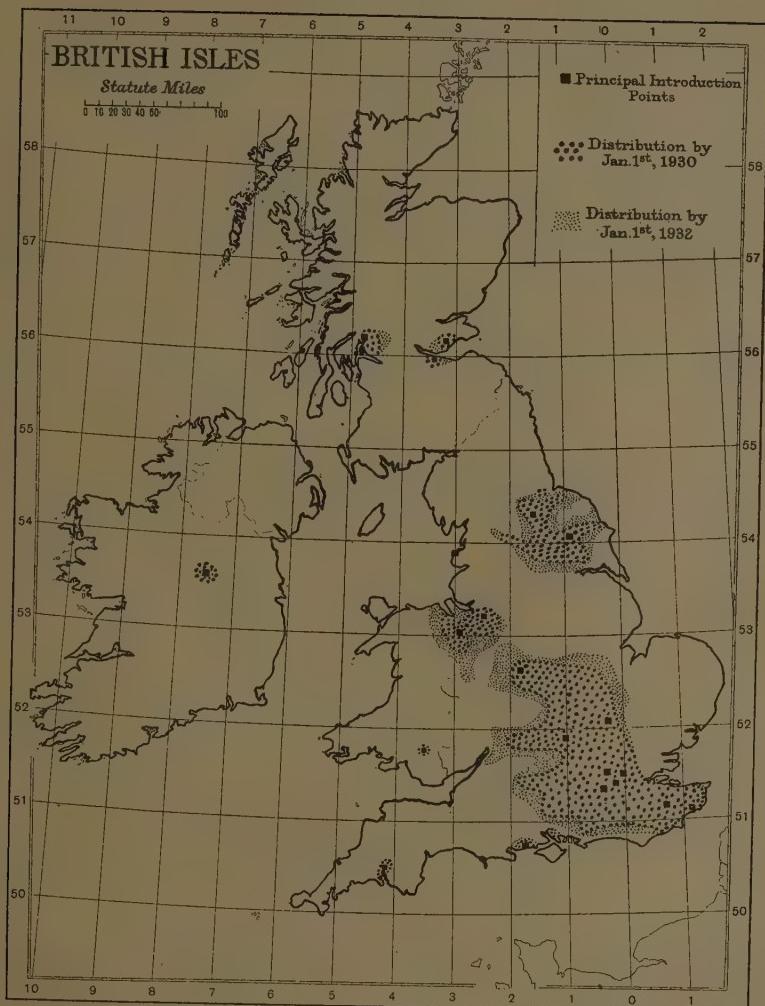
No squirrels were examined during an authentic epidemic, but specimens obtained during the late spring and summer of 1931 from Yorkshire, Cheshire, Oxfordshire, Berkshire, Hertfordshire, Buckinghamshire, and Kent all showed a chronic intestinal infection with a species of *Eimeria* (Coccidia). It is thus possible that coccidiosis was the direct cause of the reduction in numbers, and the symptoms observed in diseased squirrels support this view.

It is probable that this fall in the grey squirrel population is the beginning of a natural cycle in numbers, similar to the cycles in other rodent populations in many parts of the world. The numbers are now at a minimum, but there is no evidence of disease, and we may expect a recurrence of the period of abundance which ended so suddenly in 1930.

1928 and 1929 were good years for beech-mast and acorns, but in 1930 the crop failed in most districts. This food shortage may have weakened the squirrels' resistance to disease in the autumn and winter, 1930-1, in certain districts.

This enquiry has been carried out with the aid of a grant from the Ministry of Agriculture and Fisheries, and information was obtained from a large number of voluntary observers, whose co-operation the author wishes to acknowledge. Full details are available in the Bureau of Animal Population.

¹ For earlier work see Middleton, A. D. P.Z.S. 1930, 809-43, and "The Grey Squirrel," Sidgwick and Jackson, London, 1931.



The range of the grey squirrel in the British Isles in 1930, and the approximate area colonised from 1930 to 1932. Most of the extension of range after Jan. 1st, 1930 occurred in the summer and autumn of that year, but grey squirrels continued to spread into several new areas during 1931, in spite of the reduction in numbers.

THE ROOKERIES OF THE ISLE OF WIGHT

BY J. F. WYNNE.

(*With two Maps and one Figure in the Text.*)

I. INTRODUCTION.

THE nature and degree of the influence of the rook (*Corvus frugilegus frugilegus* L.) on agriculture have lately received considerable attention from ornithologists, and investigations have led to the taking of a census of rookeries in various parts of the country. The Isle of Wight appeared to be a particularly interesting area for the taking of such a census, as it is probably self-contained in the nesting season so far as the rook is concerned, and it presents a considerable variety of country. A census begun in 1931 was only completed in a part of the Island, but in 1932 the whole area was covered.

II. DESCRIPTION OF AREA.

The Isle of Wight is roughly rhomboidal in shape, measuring 23 miles (38 km.) between the eastern and western ends, and $13\frac{1}{2}$ miles (20 km.) from north to south. There are some 60 miles (96 km.) of coast line, and the area is 93,931 acres, or 146.76 sq. miles (380 sq. km.). The distance from the mainland coast varies between about 2 and 4 miles (3 and 7 km.), except at the Hurst Castle spit, where it is less than 1 mile (1.6 km.).

Geology. The Isle of Wight is divided into two distinct regions by a range of chalk downs which, except for three gaps cut by rivers, forms a continuous ridge from east to west. The surface of the northern region is composed of tertiary clays, which appear to be comparatively infertile, and support less cultivated land and more woodland than do the formations in the southern region. Cliffs are absent in the northern region except round the western bays, and are largely replaced by wooded slopes.

The southern region is composed of Cretaceous Beds. Below the central chalk ridge is Upper Greensand, and then Gault; these formations also surround another chalk range to the south-east. The rest of the southern region consists of Lower Greensand, except for a band of Wealden Beds along the south-west coast, and a smaller patch of Wealden Beds at the north end of Sandown Bay. The southern range of downs falls sharply to the east and south; on the east side to the Landslip, a wooded area sloping to the sea, and on the south side to the Undercliff, where an inland cliff, 4 to 5 miles (7 km.) long and about half a mile (0.8 km.) from the sea, has been formed by landslips on the Gault. (This slipping on the Gault was also the origin of the Landslip.) Between this cliff and the sea considerable woodland is found, but for some reason little of this is marked on the Ordnance Survey Map.

A rough estimate gives an area of 45,000 acres for the northern region, 35,000 acres for the southern region, and 15,000 acres for the chalk areas.

Rivers. The rivers in the Isle of Wight are scarcely more than streams except where they develop into tidal estuaries in some parts of the north coast. The Medina, which rises in the downs above St Catherine's Point and flows north right across the Island, becomes a large tidal river between Newport and Cowes. The Eastern Yar has its source near that of the Medina, and flows north-eastwards, through the reclaimed Brading Harbour to Bembridge. The Western Yar, which almost divides West Wight from the rest of the Island, flows through tidal marshland to Yarmouth. The Newtown River, between Yarmouth and Cowes, is also a tidal estuary, formed by the convergence of a number of small streams, and Wootton Creek, between Cowes and Ryde, is another tidal inlet. There are practically no streams flowing to the south and east coasts of the Island, although there are a few small ones along the south-west coast, which enter the sea through formations locally known as Chines.

The highest points in the Island are on the southern downs, where St Boniface Down above Ventnor reaches 787 ft. (237 m.) and St Catherine's Down 780 ft. (234 m.). The central ridge rises to 701 ft. (211 m.) west of the Medina River, and to 444 ft. (133 m.) east of that river, but the rest of the Island is for the most part low-lying (though somewhat undulatory), especially to the north-west and in the Eastern Yar valley. All the towns are on the coast, except Newport the capital, which is near the centre of the Island, at the head of the Medina estuary, and all are in the eastern half of the Island.

III. THE ROOKERIES.

4209 nests were counted in 1932. It was not always possible to define a distinct rookery without knowledge of the birds' feeding grounds and other factors, which have not yet been investigated, but for convenience they were mapped as 74 units, which may be classified as follows:

Table I. *Distribution of sizes of rookeries.*

| 1- 20 nests | | 20 rookeries |
|-------------|-------------|--------------|
| 21- 40 " | | 17 " |
| 41- 60 " | | 12 " |
| 61- 80 " | | 7 " |
| 81-100 " | | 6 " |
| 101-120 " | | 4 " |
| 121-140 " | | 0 " |
| 141-160 " | | 5 " |
| 161-180 " | | 1 " |
| 181-200 " | | 1 " |
| 201-220 " | | 0 " |
| 221-240 " | | 0 " |
| 241-260 " | | 0 " |
| 261-280 " | | 0 " |
| 281-300 " | | 1 " |

Average number of nests per rookery: 57.

Thus exactly half the rookeries contain less than 40 nests. There are none between 121 and 140, but five between 141 and 160. The one exceptionally large rookery, which is in a large private garden near Wootton Creek, contained some 370 nests in 1931, but had become reduced to 300 in 1932, owing, it is said, to a number of the birds being poisoned during the winter.

Water. It is quite obvious that rooks have a partiality for water, but in the Isle of Wight this partiality is apparently not confined to fresh water. The following table, though somewhat arbitrary, gives some idea of the distribution of nests in the two regions in relation to fresh-water streams, the open sea, and tidal estuaries. For the purposes of constructing this table it has been assumed that each rookery is influenced as to its position by one of

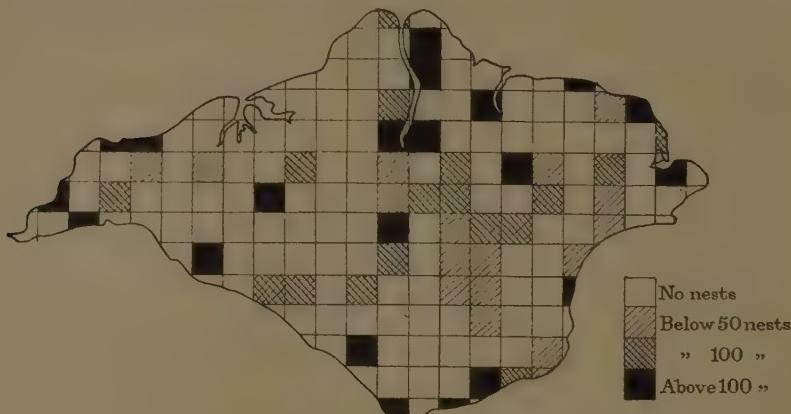


Fig. 1. Diagram to show density of nests in one-mile squares.

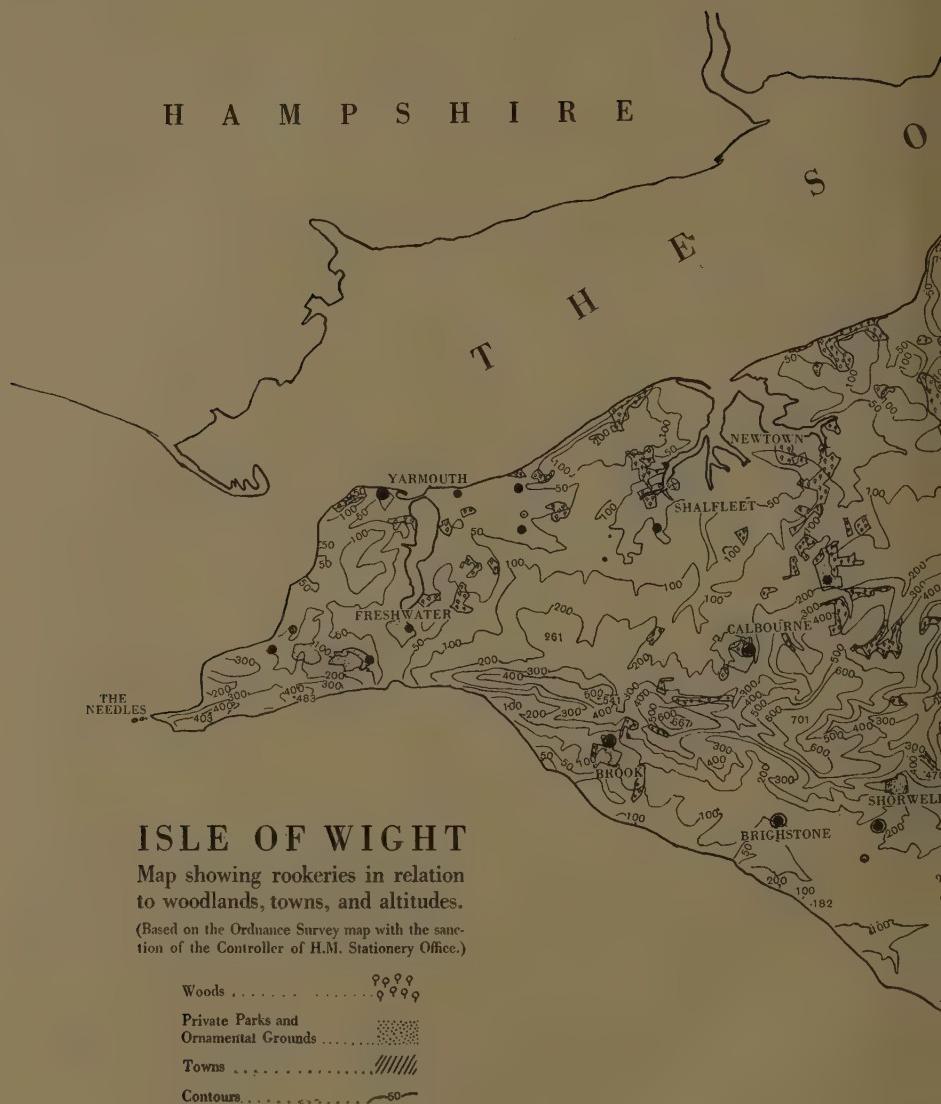
these three factors, but actually there may be a few rookeries which are not dependent on any of them. This applies particularly to some of those which have been included in the streams total. In cases where the rookery is near more than one of the three features, that which appears the most likely to be the influential factor has been selected.

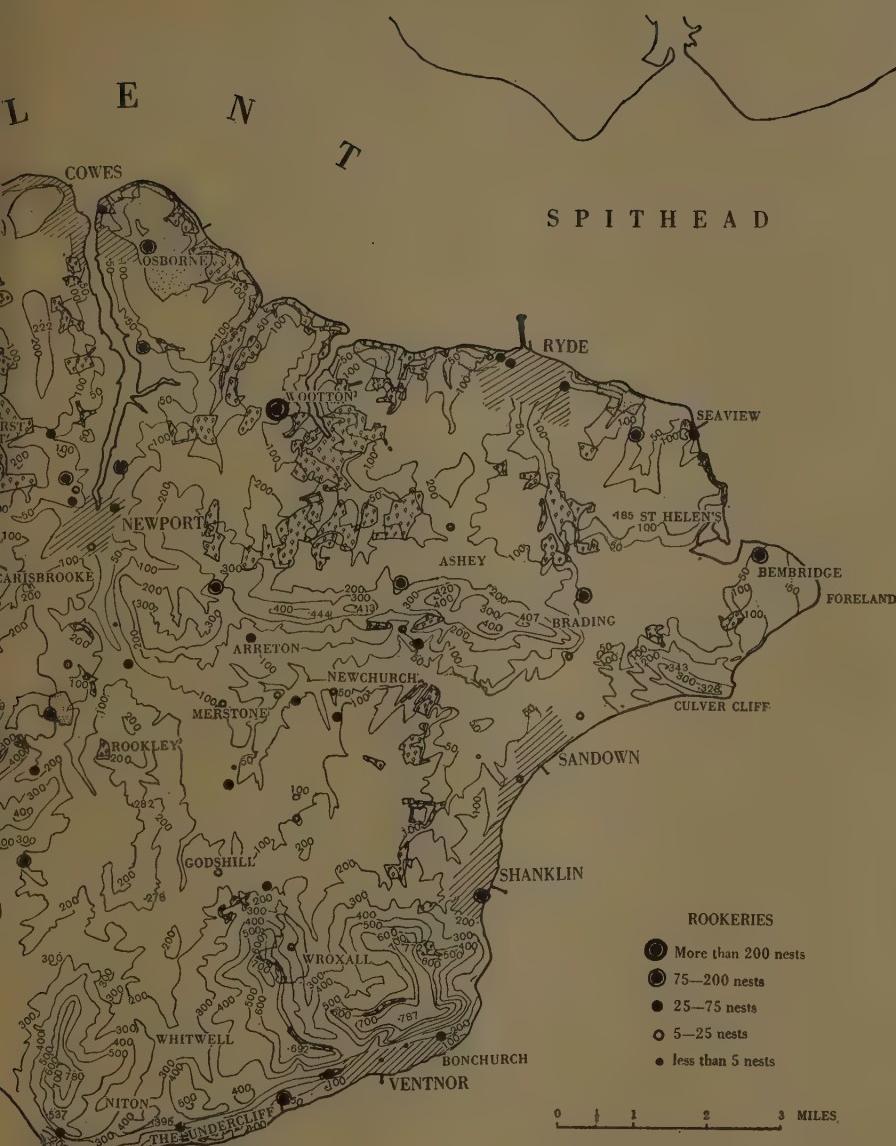
Table II. *Distribution of rookeries in relation to water.*

| | Nests near fresh-water streams | Nests near open sea | Nests near tidal estuaries | Total |
|-----------------|--------------------------------------|------------------------|-------------------------------|-------|
| Northern region | 737 | 861 | 842 | 2440 |
| Southern region | 1297 | 472 | 0 | 1769 |
| Total | 2034 | 1333 | 842 | 4209 |

This matter will be dealt with further in the geology section.

Buildings. There is a definite tendency of rooks to nest near human habitations, and it will be seen that there are quite a number of rookeries actually





C H A N N E L

ST CATHERINE'S POINT

in the towns. Most of the larger rookeries are in private grounds, especially near large old houses.

Table III. *Distribution of rookeries in relation to buildings.*

| | Northern region | | Southern region | | Total | |
|--------------------------------------|-----------------|-------|-----------------|-------|-----------|-------|
| | Rookeries | Nests | Rookeries | Nests | Rookeries | Nests |
| In towns | 11 | 429 | 5 | 170 | 16 | 599 |
| Near large houses in private grounds | 8 | 1100 | 9 | 674 | 17 | 1774 |
| Farms | 1 | 86 | 9 | 373 | 10 | 459 |
| Near other houses or in villages | 13 | 514 | 16 | 345 | 23 | 859 |
| Not near buildings | 3 | 311 | 8 | 207 | 11 | 518 |
| Total | 36 | 2440 | 41* | 1769 | 77* | 4209 |

* The rookeries of the southern region were counted as 38, but for the purposes of the above classification two have been split up.

In view of the fact that the northern region is less fertile than the southern there are probably less farms, which will account for the paucity of nests near farms in the northern region.

Geology. The choice of nesting sites is obviously influenced by the character of the geological formations, presumably indirectly through their influence on the birds' feeding grounds. From a glance at the geological map it will be seen at once that there are large regions in the northern area completely devoid of rookeries. This applies particularly to the areas covered by the Hamstead Beds, Bembridge Marls and Bembridge Limestone. There are several rookeries on the Osborne, Headon and Bagshot Beds in the west, and it is a somewhat remarkable fact that where the Osborne Beds reappear to any extent, namely on the north-east coast in the vicinity of Ryde and Seaview, and at East Cowes and Osborne, there is a considerable concentration of rookeries.

Table II shows that there is a considerable concentration of rookeries near salt water, especially near the tidal estuaries, and it would therefore appear that the neighbourhood of these estuaries offers particularly good feeding grounds, partly perhaps, in the mud-flats which are exposed at low tide in the creeks.

Agriculture. The following table is of some interest, though I have only been able to obtain statistics for the Island as a whole:

Table IV. *Agricultural statistics.*

| | | | | | | | |
|---|-------------------------|-----|-----|-----|-----|-----|----------------|
| Area of Isle of Wight | ... | ... | ... | ... | ... | ... | 93,931 acres |
| Arable land, 1930 | ... | ... | ... | ... | ... | ... | 21,502 " |
| Cereals | 9,740 acres | | | | | | |
| Other crops | 11,202 " | | | | | | |
| Bare fallow | 560 " | | | | | | |
| Land under grass, 1930 | ... | ... | ... | ... | ... | ... | 40,289 " |
| Total arable and grassland, 1930 | ... | ... | ... | ... | ... | ... | 61,791 " |
| Spring rook population in the Isle of Wight, 1932 | ... | ... | ... | ... | ... | ... | c. 8,418 birds |
| Average birds per acre | ... | ... | ... | ... | ... | ... | 0.09 |
| " | of arable and grassland | ... | ... | ... | ... | ... | 0.136 |
| " | of arable land | ... | ... | ... | ... | ... | 0.391 |
| " | of cereals | ... | ... | ... | ... | ... | 0.863 |
| " | of other crops | ... | ... | ... | ... | ... | 0.76 |

ISLE OF WIGHT

Map showing the rookeries in relation to chief geological formations and streams.

(Based on the Ordnance Survey map with the sanction of the Controller of H.M. Stationery Office.)



Map 2.

The averages shown in the above table are so small that it would appear improbable that the rook can have any very great effect on agriculture.

Altitudes. The following table shows the approximate numbers of nests within intervals of 50 ft. above sea-level.

Table V. *Distribution of altitudes of rookeries.*

| | | | | |
|------------|--------------------------|-----|-----|-----------|
| Sea-level: | 50 ft. (0- 15 m.) | ... | ... | 700 nests |
| | 50-100 ft. (15- 30 m.) | ... | ... | 1200 " |
| | 100-150 ft. (30- 45 m.) | ... | ... | 1000 " |
| | 150-200 ft. (45- 60 m.) | ... | ... | 950 " |
| | 200-250 ft. (60- 75 m.) | ... | ... | 150 " |
| | 250-300 ft. (75- 90 m.) | ... | ... | 150 " |
| | 300-350 ft. (90-105 m.) | ... | ... | 45 " |
| | 350-400 ft. (105-120 m.) | ... | ... | 0 " |
| | 400-450 ft. (120-135 m.) | ... | ... | 37 " |

These figures are exclusive of the heights of the nests in the trees.

It will be seen from this table that about 90 per cent. of the nests are below 200 ft. (60 m.). The 37 nests between 400 and 450 ft. (120 and 135 m.) are in the Undercliff region at Blackgang, and are in a remarkably exposed position, only sheltered from the full force of the prevailing winds by a belt of small wind-blown trees.

Trees. Nests were found in 23 species of trees, but nearly 90 per cent. were in Elm (Common and Wych), Oak, Scots Pine, Ash and Beech. 108 of the 279 nests in Beeches were in one rookery. There were nine typical hedgerow and roadside Elm rookeries, comprising some 400 nests. There were also seven rookeries composed exclusively of Oaks, three of Scots Pines, and one of Ashes. There were nine rookeries of Elms alone in addition to the nine hedgerow rookeries, several in which the majority of the nests were in Elms, and two or three in which the majority were in Oaks. There were seven nests in a dead Scots Pine in one rookery, and two in a tree of the same species in another.

Table VI. *Trees in rookeries.*

| | No. of rookeries in which represented | No. of trees | No. of nests | Av. nests per tree | % of total |
|------------------------------|--|-----------------|-----------------|-----------------------|------------|
| Elm (Common and Wych) | 55 | 547 | 1812 | 3.31 | 43 |
| Oak | 25 | 167 | 756 | 4.52 | 18 |
| Scots pine | 20 | 130 | 540 | 4.15 | 13 |
| Ash | 24 | 98 | 357 | 3.64 | 8.5 |
| Beech | 19 | 81 | 279 | 3.44 | 6.5 |
| Stone pine | 4 | 11 | 82 | 7.45 | 2 |
| Lime | 8 | 24 | 81 | 3.38 | 2 |
| Horse chestnut | 6 | 17 | 59 | 3.47 | |
| Sycamore | 7 | 25 | 52 | 2.08 | 4 |
| Ilex (Holm oak) | 6 | 10 | 50 | 5.00 | |
| Others (13 species) | — | 42 | 133 | — | |
| Unidentified (all deciduous) | — | 3 | 8 | — | |
| Totals | | 1155 | 4209 | 3.73 | |

The 13 species not specified consist of the following:

Cypress species: 40 nests in four trees (in two rookeries).
Poplar species: 17 nests in one tree.
Austrian pine: 16 in one tree.
Larch: 15 in twelve trees (all except one in one rookery).
Plane: 12 in six trees (all except one in one rookery).
Alder: 11 in nine trees (two rookeries).
Sweet Chestnut: 5 in three trees (one rookery).
Hornbeam, Spruce Fir and Willow species: each four nests in one tree.
Bay: three nests in one tree.
Wild Cherry and Acacia (*Robinia pseudacacia*) each one nest.

A full list of the rookeries has been deposited with the Oxford Bird Census.

IV. SUMMARY.

1. A census was taken of the rookeries in the Isle of Wight in 1932. 4209 nests were counted, giving a spring population of about nine birds per 100 acres over the whole area.

2. The rook has an obvious partiality for nesting in the neighbourhood of fresh water streams, but there appears also to be a marked tendency to build near salt water.

3. The neighbourhood of buildings is favoured, especially of old houses in large gardens and parks; rookeries in the towns are frequent.

4. The distribution of rookeries is definitely influenced by the character of the geological formations.

5. The low average of birds per acre of crops suggests that it is improbable that the rook can have any real effect on agriculture.

6. About 90 per cent. of the nests are below 200 ft. (60 m.) above sea-level.

7. Nests were found in 23 species of trees, 43 per cent. being in Elms, and nine nests in dead Scots Pines.

V. ACKNOWLEDGMENTS.

I am much indebted to Mr W. B. Alexander for invaluable assistance in the field, and for advice on the preparation of this paper, and to Mr G. G. Hartill for assistance in the field and ringing a number of nestlings; also to Messrs H. M. Livens, H. White, R. Drake, J. M. Goodall, Miss M. A. Orme, and others for assistance in 1931.

SOME ECOLOGICAL FACTORS AND THEIR INFLUENCE ON COMPETITION BETWEEN STREAM AND LAKE-LIVING TRICLADS

By R. S. A. BEAUCHAMP.

(Assistant Naturalist at the Laboratory of the Freshwater
Biological Association.)

(With nine Figures in the Text.)

THE normal habitat for *Planaria alpina* is a fast flowing stream, but this species has also been recorded on shores of lakes in the Alps and Tatra Mountains (5, 9, 11, 17, 18). According to a number of these workers it is found on the "Brandungszone," that is to say, on the wave-washed shores. The object of this paper is to analyse the factors, both physical and bionomic, which limit the occurrence of this species to this type of shore. In this country observations can only be made in winter, since the high summer temperature prevents the stream planarians from colonising the lake shores.

A short description of the area investigated is necessary. The focus of attention is a delta of loose stones formed by a fast flowing stream (High Wray Beck) where it enters Blelham Tarn. The upper reaches of the stream contain *Pl. alpina* in large numbers and a few *Polyclelis cornuta*. One branch of this stream, though not fed by a true spring is more permanent than the others, and contains most of the planarians. The other branches are more rapidly affected by heavy rains, which fact shows the more superficial nature of their water supply. They contain few planarians and these occur not in the main branches but in small trickles which find their origin in tiny springs along the course of each stream as well as near its source.

The lake itself is about 825 yards (750 m.) long and at its widest about 330 yards (300 m.). Its long axis lies north-east—south-west so that south-west winds blowing along the lake can soon make it very rough.

The delta under consideration lies on the south side of the east end of the lake and faces north-west. From the map (Fig. 1) it will be seen that opposite this delta on the other side of the lake is another stream down whose valley the north-west winds blow, across the lake, straight on to the delta.

Fig. 2 is a map of the delta, showing contours and nature of substratum. The area is bounded on its two sides by muddy banks of *Phragmites* and *Carex*. These plants show the succession characteristics of a slightly acid lake. *Phragmites communis* forms the outer edge of the swamp which surrounds the greater part of the lake. This is replaced by *Carex inflata* which in turn gradually gives place to a fringe of *Carex elata*. The proximity of this zone of

vegetation is important since it forms a sharp boundary to the stony delta which is the temporary habitat of the stream planarians described in this paper.

The heavily marked contour at the top of the map (contour 7) is the level reached by the lake after a heavy rainfall. An exceptional flood will rise to contour 8.

The higher part of the delta is marked *A*, and consists of a flat pile of loose stones which falls away steeply into the water at its lakeward face. This mass of stones was brought down in a late summer flood and deposited in the mouth of the original stream. A subsequent deposition of stones at *C*

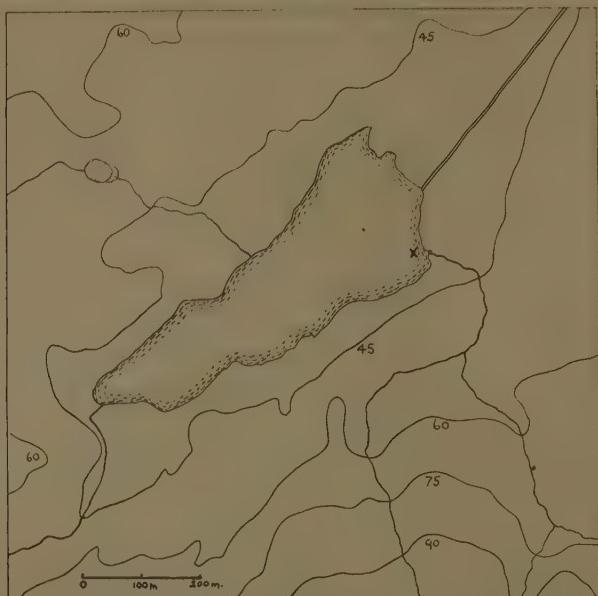


Fig. 1. Map of Blelham Tarn, Westmorland. *X* marks the position of the delta formed by High Wray Beck. This area is 1 sq. km.

during an exceptionally high flood at the beginning of October deflected most of the stream to the right.

The small bay *a* on the landward side of the delta is protected from the stream by clumps of *Juncus effusus* and the bank of grass (*Holcus lanatus* and *Deschampsia caespitosa*) immediately behind it. It is also protected from wave action since it lies at a lower level than the main delta *A*.

The area marked *B* is about 8 in. (20 cm.) lower than the big pile of stones *A* and consists of a sprinkling of stones on a relatively firm substratum of sand and coarse mud. Near the lakeward edge of this area there are many more stones. This whole area *B* is out of the main flow of the stream and on account of its lower level is free from wave action except at periods of very low water.

C is a pile of stones similar to the main delta *A* but consists of slightly larger stones; it is smaller in area and is at a higher level than *A* as is shown by the contours.

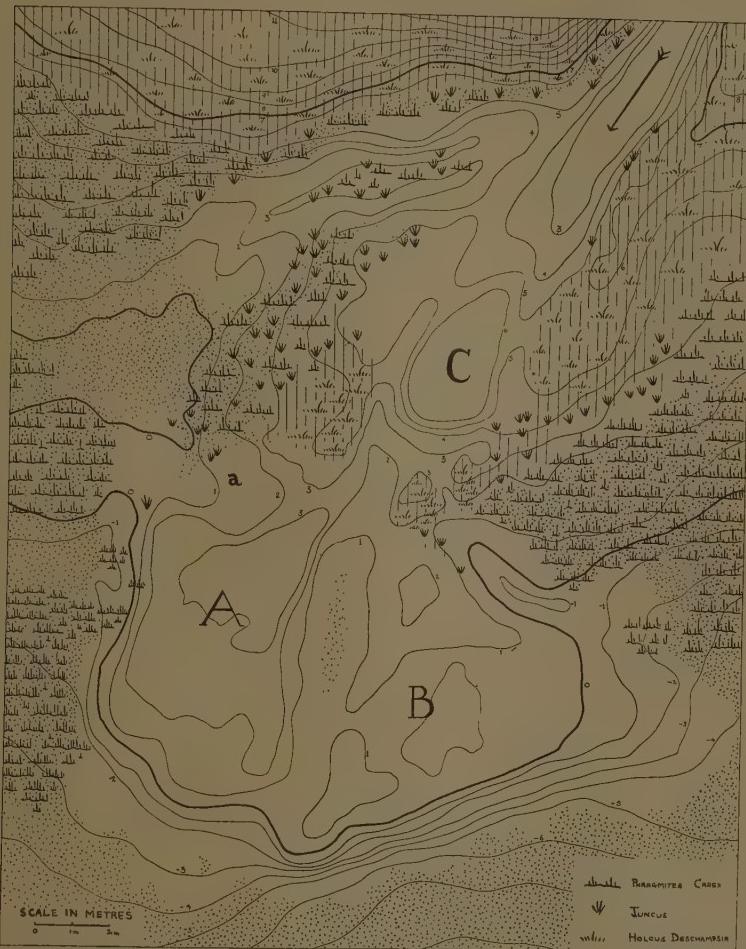


Fig. 2. Detailed map of the delta formed by High Wray Beck, showing contours, vegetation and nature of substratum. The areas left white are covered with loose stones.

Contour 0 marks the lowest level of the lake; below this level is found the permanent planarian fauna. It was necessary to use a pair of tongs to lift the stones from this area except when the water was at its lowest.

The limnophile Triclad found here are *Planaria lugubris*, *Polyclelis nigra* (14, 19) and *Bdellocephala punctata*. *Pl. lugubris* tends to remain at a greater depth than either of the others. *Pol. nigra* is found in greatest numbers near the reeds. *Bd. punctata* mixes freely with the *Pl. lugubris* zone but extends further towards the shore. As the level rises so do these species advance landwards wherever conditions are suitable.

The most active migrations are made by *Pol. nigra*. Individuals of this species have been found in swampy places 55 yards (50 m.) inland from the summer limit of the lake, soon after the first autumnal rains had raised the level of the lake sufficiently to swamp the surrounding low-lying areas. This species also migrates across stony areas and is always to be found on the area *B*. This capacity for making quick migrations, together with the general hardy character of this species, may account for its wide geographical distribution. According to Becklemischev (3) it is the only species found in the area between the Volga and the Yenessei.

The migrations of *Bd. punctata* are restricted to relatively stony areas which are out of the current. With occasional exceptions this species is confined to the outer fringe of the delta *A*, and to the area *B*, which under normal winter conditions is almost permanently covered with water. There exists some difference of opinion as to the most suitable conditions for this species. Krzysik (15) says muddy, and Demel (6) says stony substrata are preferred. It may be found on either, as well as on leafy deposits; probably the substratum is not a very important factor for this species.

The area colonised by *Pl. lugubris* extends only slightly above the low level contour; probably this is due to its rather special requirements, namely, a few stones on a muddy bottom. The area *B* appears to be a suitable place for this species and, indeed, some individuals can be found on it, but not nearly so many as one would expect if there was a general spreading out from the deeper water. This scarcity may be explained by the very stony nature of the lake-ward edge of this area.

After heavy rain the level of the lake will rise rapidly two or more feet, completely covering the area *A*. The upper reaches of the stream are greatly affected and are soon thrown into a state of full spate. Many of the planarians, besides insect larvae and Gammarids, are swept down-stream and are deposited on the delta. After a storm of rain the whole delta is under water.

Individuals of *Pl. alpina* constitute almost the whole of the stream planarian population. There are very few *Pol. cornuta* in this stream and consequently very few are washed down. On one or two occasions *Pl. vitta* (21) was recorded on the delta.

The planarians washed down can establish themselves only in places where the substratum is suitable and where there is no current or wave action. As the rain is usually accompanied by wind, which soon agitates the surface of the lake, it is only where the current has been damped down and where the

water is calm, or more precisely where the substratum is free from wave action, that the planarians establish themselves.

Fig. 3 shows the condition found just after one of these floods. There are considerable collections of *Pl. alpina* in the areas which are out of the current and which are also sheltered from wave action, notably at *a*.



Fig. 3. General view of delta showing areas where *Pl. alpina* (=■) first establish themselves after being washed down-stream. Shaded area unsuitable for colonisation.

If calm weather follows, these groups of planarians soon spread out in all directions, except, of course, where conditions are quite unsuitable for these lithophilous forms. Fig. 4 shows how the whole of the delta *A* has been colonised in this way.

A point of interest, which will be considered again, is the fact that none of these planarians which normally live in the fast flowing upper reaches of

the stream, make any attempt to go up-stream. Moreover careful laboratory experiments show them to be negatively rheotactic.

During the calm weather following the rains the water level sinks and the planarians keep pace with the water line. Fig. 5 shows the line of planarians coincident with the water level. Long search showed no isolated individuals on

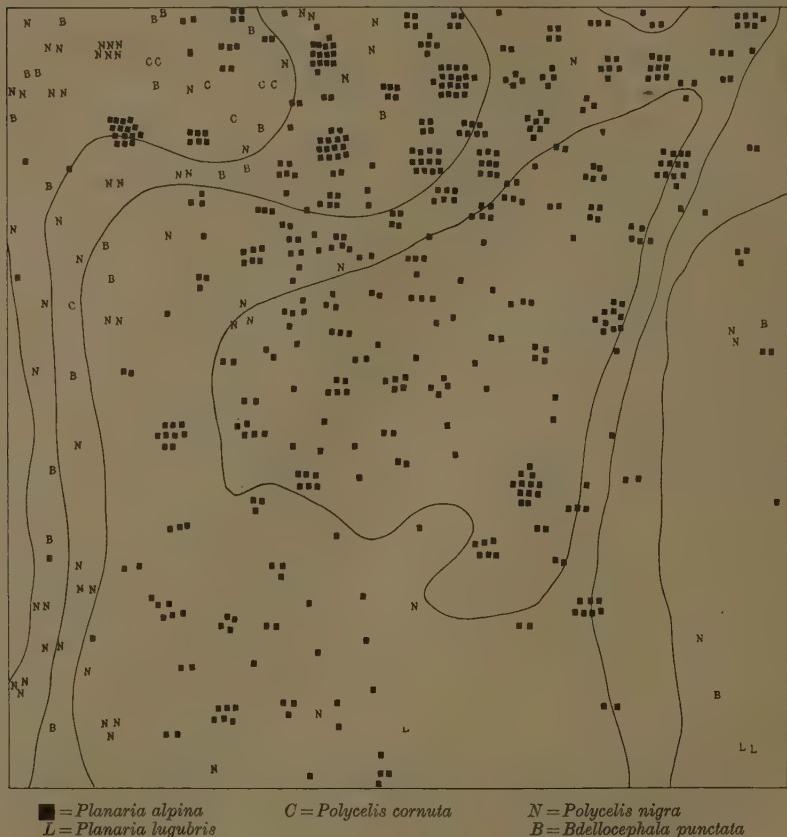


Fig. 4. Shows even colonisation of the area A. During calm weather this condition follows that shown in Fig. 3.

the drying stones and, though absolute accuracy of numbers cannot be hoped for in such a large area, the actual numbers recorded in Figs. 4 and 5 show a rough agreement.

If, after this stage, the water rises gradually these animals migrate in all directions, and soon the area A is more or less evenly re-colonised, so that it returns to a condition resembling that shown in Fig. 4.

On the other hand, if the rise is rapid and a considerable disturbance is set up, many of the *Pl. alpina* are swept off the delta presumably into the lake, where they soon die owing to the unsuitable nature of the bottom.

If a storm of wind arises, especially from the north-west, which as we have seen blows straight on to this delta, all the planarians above a certain depth



Fig. 5. Ring of migrating planarians coincident with retreating water line.

are dislodged. Fig. 6 shows the condition on December 6th—the delta *A* is evenly colonised by *Pl. alpina*. This condition arose in the usual manner, namely, after flooding (on December 4th), the planarians which were brought down migrated out from the centres where they had been deposited, notably from *a*, and colonised *A*.

Fig. 7 shows the condition on the following day (December 7th). The height

of the water had decreased slightly by the second day but the important point was that on the night of the 6th there had been a storm of wind from the north-west. The result was that all the planarians on the top of the delta were dislodged. Some of these animals may have been swept quite passively into

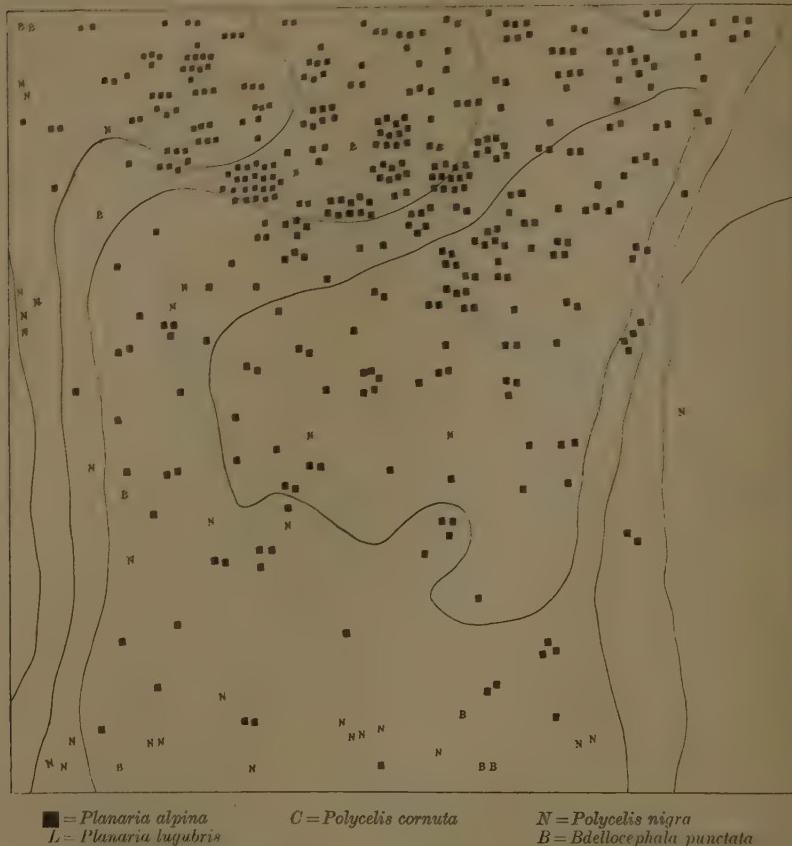


Fig. 6. Shows even colonisation of the area *A*; compare with Fig. 7 which represents the condition found on the following day after a storm of wind.

sheltered places but most likely the majority on being disturbed by the wave action wandered about until they found themselves in a sheltered place. The small bay *a* is the only sheltered area which is close to the main delta *A* and consequently it was here that all the planarians collected. Previous to the storm of wind there was in *a* only a moderate population of *Pl. alpina*, comparable in density to that on the delta *A*. This particular instance which is

typical of many others, shows very clearly the inability of *Pl. alpina*, as well as the other limnophile planarians represented on Figs. 6 and 7 to withstand strong wave action.

The last stage, dependent on the gradual lowering of the level of the lake to something approaching its lowest winter level, has yet to be considered.

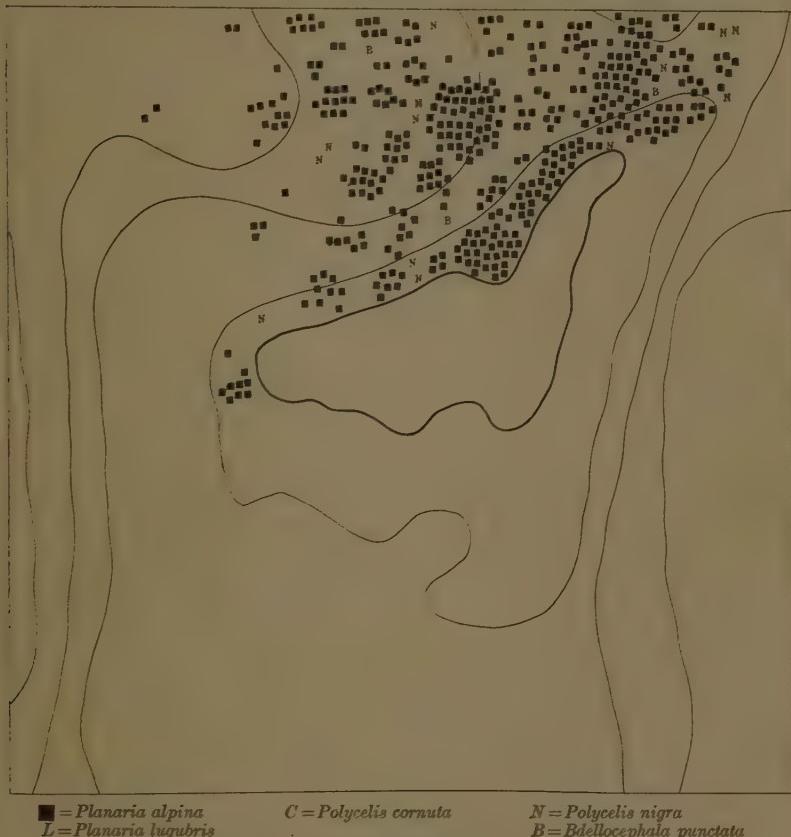


Fig. 7. The effect of wave action on the area A. The day before, this area evenly colonised, see Fig. 6.

The sequence so far has been: the planarians are washed down and deposited on certain centres: they wander in all directions from these centres, and follow the gradually changing water level. As has been shown, these stages are greatly affected by storms of wind or rain.

If the water level continues to fall, the "ring formation" shown in Fig. 5 is followed by the condition represented in Fig. 8 which is remarkable for the



Fig. 8. The final stage dependent on the lowering of the water level, showing disappearance of *Pl. alpina* and increase in numbers of *Pol. nigra*.

sudden disappearance of *Pl. alpina* and the equally rapid increase in the numbers of *Pol. nigra*.

An almost exactly similar series of events occurs on the pile of stones marked *C*, Fig. 2. But since this area is at a high level, the initial flood has to be very heavy before the planarians, which are washed down-stream, can be deposited in the sheltered places on, or in the immediate neighbourhood of this area.

But after a high flood has covered the whole of this area, the same series of events, dependent on the sinking of the water level and on wave action, occurs as was described for the main delta *A*. The only difference being that the last stage, which was represented on the delta *A* by the disappearance of the *Pl. alpina* and the huge increase in the numbers of *Pol. nigra*, does not occur on this area *C*. This can be explained on two counts. Firstly, because *C* is rather far removed from the reeds where the majority of the *Pol. nigra* live. And secondly, because as the level of the water falls, the two streams which flow on either side of this area are re-formed. These streams prevent what *Pol. nigra* there are from reaching *C*, since this species avoids a current. These streams also lead to the gradual dispersal of the *Pl. alpina* from this area down-stream, since, as before stated, these individuals are all negatively rheotactic. Nevertheless during the periods of low water a few can usually be found on the sheltered landward side of this area.

The relation in time between the stages on the two areas *A* and *C* is much as one would expect. At first the animals carried down by the main stream are deposited on the lakeward face of the delta. But as the level of the lake rises this "area of deposition" advances landwards, so that only at the end of the flood when the water level has risen to cover the area *C* does this area receive any of the animals. In all the subsequent stages, dependent on the sinking of the water line, the area *C* will, of course, be ahead of the area *A*.

At the beginning of the paper it was pointed out that the area *B* (see Fig. 2) supported a planarian fauna consisting of the three limnophile species (*Pl. lugubris*, *Pol. nigra* and *Bd. punctata*). These individuals are colonists which have migrated from their permanent habitat, which is situated immediately below the lowest summer level.

This area *B* is also colonised by members of the stream fauna which have been washed down. It is sheltered from strong currents by the banks of *Juncus* to landward and from wave action since it lies about 8 in. (20 cm.) lower than the rest of the delta, consequently it forms a refuge to which planarians find their way from the more exposed areas.

DISCUSSION.

Various continental workers (5, 9, 11, 17, 18) have recorded *Pl. alpina* in lakes in the Alps and Tatra Mountains and they say that this species is found in the "Brandungszone." From this fact some of these workers have concluded that wave action is a necessary factor for the well being of this species, taking the place of the running water in their more usual habitat.

From what has been said in this paper it would seem that wave action is the one thing that this species (or any other species of planarian) cannot tolerate.

It is known that *Pl. alpina* cannot live on sand or mud; or, more exactly, it has never been recorded except from stony substrata. It would seem therefore that *Pl. alpina* establishes itself on rocky shores not because it requires the constant water movements but because it cannot live in quiet places which are of necessity either muddy or sandy. But it can avoid the more violent action of the waves by keeping at a sufficient depth though still remaining on stones free from silt. The various workers do not state at what levels they found *Pl. alpina* or whether the shore consisted of stones of such a size or shape that they would not be moved about by the waves. This last point is probably of considerable importance. During the winter months *Pl. alpina* can be found under the stones on the shores of Windermere—where the stones are for the most part of a fair size and rather flattened.

The way in which the *Pl. alpina* leave stones which are disturbed has been demonstrated by their various migrations on the delta; in another way this reaction is very evident. If, when examining the delta, the stones were lifted roughly the planarians nearly always fell off. Although very great care was taken to prevent this happening, even so, one had to be on the look out for any that might still fall off. This reaction may be of significance in saving them from being crushed between moving stones.

When examining a stream, the same tendency to fall off is not apparent. At first sight it seems surprising that the normal behaviour can alter so quickly and so radically to suit new environmental conditions. A very simple experiment provided the explanation. A number of *Pl. alpina* was collected from a fast flowing stream; these individuals showed no tendency to fall off the stones. They were put into a basin containing a few stones. They settled down under the stones. After they had been there a day the stones were lifted—in all cases large numbers of them fell off. Moreover, before lifting the stones, a few of the planarians could be seen to be weakly fastened on, some lying with only one side of the body attached to the stone.

The conditions during the experiment had been entirely suitable with regard to light and temperature and the animals had been kept in their own spring water. One had laid a cocoon and one pair had been found copulating so there was no question of them having become unhealthy, owing to con-

ditions during the experiment. The important factor which caused them to fall off was the quiet conditions preceding the lifting of the stones. Under absolutely quiet conditions they do not fasten themselves on in the same way as they do when they settle down in a current, consequently a sudden movement finds them unprepared. Exactly the same principle applies to their behaviour on the delta where they had settled down under quiet conditions and consequently were not firmly attached to the stones, the lifting of the stones causing them to fall off. The development of waves may have the same effect.

A remarkable fact, which has been mentioned already, is that none of the planarians which have been washed down shows any tendency to go up-stream again. A number of workers have studied rheotaxis in *Pl. alpina* and other species of stream living planarians (4, 7, 11, 13, 16, 20). There exists considerable difference of opinion. Steinmann and Doflein found them to be positively rheotactic; Carpenter found them to be negatively rheotactic; Pearl found the species he was working with (*Pl. dorotocephala*) indifferent.

It seems unlikely that a stream living planarian could be consistently negatively rheotactic, nor for that matter can we suppose that they are continually positively rheotactic. Experiments (1) show that their behaviour changes with the age and physiological condition of the individual animal. There was also an indication that those which are negatively rheotactic are also less efficient at holding on. This fact must be of great significance when considering, as in this particular case, a population consisting of planarians which have been washed down from their normal habitat. It leads one to expect a population with a high percentage of negatively rheotactic forms, which is indeed the case.

There is no reason for supposing that these individuals which have been washed down are incapable of re-establishing themselves. On the contrary during the winter months there is on the area *B* a constant though small population of *Pl. alpina* which seems to be in equilibrium with the rest of the planarian fauna there. And again during the winter *Pl. alpina* can be found on the shores of some of our larger lakes. The only reason why *Pl. alpina* cannot become a permanent member of the fauna of lake shores in this country is because of the high summer temperature.

The last stage following the sinking of the water level on the delta *A*, when the *Pl. alpina* disappeared and the number of *Pol. nigra* increased, remains to be explained. *Pl. alpina*, as we have already seen, is capable of establishing itself during the winter months on the area *B* and on shores where the physical conditions are suitable. By physical conditions are meant substratum, temperature and chemical composition of the water. Fig. 9 shows graphs of the temperature and pH values for the lake during the time that this work was done. The temperatures recorded are all well below 15° C., the maximum temperature at which *Pl. alpina* is found under natural con-

ditions. The pH values vary only slightly and, moreover, in very soft waters such as those under discussion, changes in hydrogen ion concentration are not of the same significance as in hard water.

The consideration of one special feature of this area may afford an explanation of the peculiar end to the activities of *Pl. alpina* on the delta A. Namely the very limited stony area and the very close proximity of the reeds which are the home of most of the *Pol. nigra* and which form a most unsuitable habitat for the *Pl. alpina*. Consequently, as the water level falls, the available stony area is greatly reduced. The *Pl. alpina* and the other planarians on the delta A become very overcrowded. The available food is soon eaten and it is not unlikely that the planarians start eating each other.

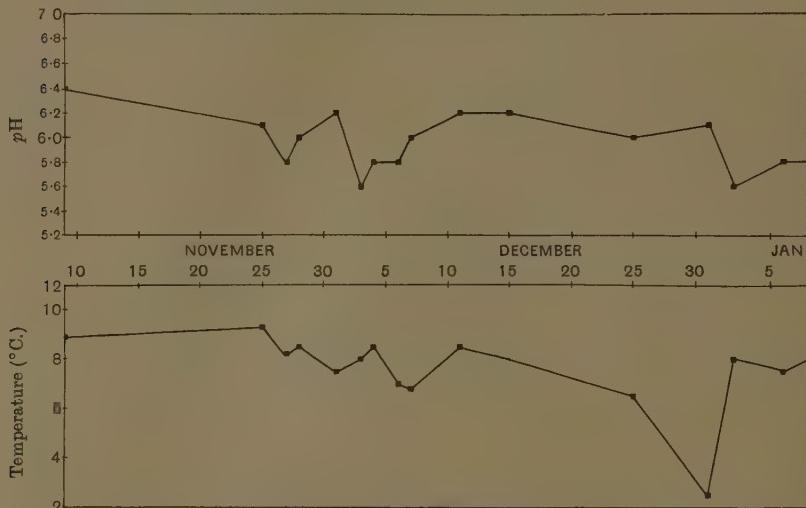


Fig. 9. Graphs showing day temperatures and the pH values of lake and stream during the winter months.

In fact, it is known that planarians will sometimes eat other planarians, whether they belong to the same or to different species (12, 16). According to Pearl, "A partially crushed specimen of planarian, even though still able to move about, will be seized upon and eaten as quickly as any other food. I have several times seen specimens thus eaten. It is, in fact, possible, with a little patience, to make a specimen eat a small piece cut off the posterior end of its own body" (p. 535).

It seems possible therefore that the *Pl. alpina* may be eaten by the *Pol. nigra*. Unfortunately no evidence of a positive nature could be obtained on this point. It is extremely rarely that one ever finds a dead planarian, as on dying they usually disintegrate (8). If in this case they are being devoured, one would be very unlikely to find remains, as a planarian's method of feeding,

namely by external digestion, would greatly assist the already rapid process of disintegration. Direct observation is almost impossible as these activities take place for the most part under the stones and during the night. Completely negative results were obtained from experiments in the laboratory where numbers of both species were kept together under as natural conditions as possible.

That the *Pol. nigra* are in very good condition is suggested by their pitch black colour, which according to Voigt (22) indicates that they are living under optimum conditions. Whether the *Pol. nigra* devour the *Pl. alpina* or not, it seems evident that *Pl. alpina* cannot live in too close competition with *Pol. nigra*. This would seem to be an additional factor in limiting *Pl. alpina* to the "Brandungszone" where *Pol. nigra* is rarely found.

SUMMARY.

An account is given of the planarian fauna on a small delta formed by a stream where it flows into a lake, Blelham Tarn, Westmorland. The migrations of the lake-living forms are shown to be dependent largely on the nature of the substratum.

Stream planarians which are washed down are capable of colonising the stony areas, but are influenced, in the same way as are the lake-living forms, by wave action. Reasons, different to those suggested by continental workers, are given for the occurrence of *Planaria alpina* on the "Brandungszone": these include the absence of competition with *Polycladis nigra*.

My thanks are due to Dr W. H. Pearsall of Leeds University for naming the plants in the area and to Mr P. Ulyott, Assistant Naturalist at the Laboratory of the Freshwater Biological Association, for much help.

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NOTES

PERIODIC FLUCTUATIONS IN THE PREVALENCE OF THE WHEAT BLOSSOM MIDGE.

It is now well known that certain mammals, e.g. lemmings, fluctuate in numbers from time to time culminating in regular migration periods every third or fourth year. For example, Elton (1) has stated that 1918, 1922 and 1926 were lemming years in Norway. Furthermore, it has been shown that there is a ten-year cycle in fur-bearing animals in Canada. Among birds, Kloster (2) has revealed a similar cycle, in the case of the willow grouse in Norway, running parallel with that of the lemming.

Among insects, Decoppet (3) has shown that outbreaks of the cockchafer have occurred in certain parts of Europe every three years for the last sixty years, and it is recognised that such outbreaks generally occur every three or four years. In this case the periodicity may be partially explained by the long time it takes these insects to reach the adult stage. But this will not hold good for all insects which have a periodicity.

Since 1917 reporters of the Ministry of Agriculture have made observations as to the comparative prevalence of certain of the more important insect pests. In 1928 (4) an attempt was made to express diagrammatically the general nature of the fluctuations in the incidence of attack of a few typical pests for the years 1917–27. In the diagram are given the fluctuations of the plum aphid (*Anuraphis padi*), the rosy apple aphid (*A. roseus*), the woolly aphid (*Eriosoma lanigerum*), flea beetles (*Phyllotreta* spp.), the leather jacket (*Tipula* spp.), the frit fly (*Oscinis frit*), the mangold fly (*Pegomyia hyoscyami*) and the winter moth (*Cheimatobia brumata*). It must be realised that these graphs are based upon observations made by trained reporters. Fryer hesitated to make any suggestions as to the explanation of the fluctuations recorded owing to the short time over which the scheme of observation had been in operation. This is where one of the chief difficulties of dealing with insect fluctuations occurs. With fur-bearing animals it is possible to look up records over long periods in the past; with almost all insects however one has to start making observations *de novo*.

In the same publication (4) in the paragraph dealing with the wheat midges (*Contarinia tritici* Kirby and *Sitodiplosis mosellana* Géhin) it is stated that they were "especially destructive in certain districts in 1926....Previous years in which wheat midges were plentiful were 1916 and 1920."

In 1927 the writer started a quantitative study of the fluctuations of certain gall midges (Cecidomyidae, Diptera). The first part of this has been recently published (5), and deals with the infestation of a field of wheat at the Rothamsted Experimental Station, Harpenden, over the period 1927–31.

One outstanding result of this work has been to show that, although the numbers of the two species fluctuate independently of each other, considering both species together the year 1927 was characterised by the comparative scarceness of the midges. In 1928 their prevalence was considerably increased and it remained slightly above this level in 1929. In 1930, however, a decided increase again took place followed by a further definite rise in 1931. The following table will make this clear.

Prevalence of the wheat blossom midges 1927–31: (a) the percentage kernel attack, (b) the number of larvae present in 500 ears of wheat.

| | 1927 | 1928 | 1929 | 1930 | 1931 |
|-----|-------|--------|---------|--------|--------|
| (a) | 3.2 | 6.5* | 7.7* | 17.6 | 21.4 |
| (b) | 2,495 | 4,238* | 19,852* | 22,340 | 25,290 |

* In 1928 the numbers of *S. mosellana* went up, whereas in 1929 the numbers of *C. tritici* were up. This, together with the fact that the two species exhibit distinct specific characters as regards the numbers of larvae found in any one kernel, explains the disparity in the increase of the percentage kernel attack and the numbers of larvae present in 1928 and 1929 (for further details see (5)).

Attention is re-drawn to the fact that by observation 1916, 1920 and 1926 were years of outstanding prevalence of the wheat midges, and also that in the quantitative study 1931 was, if not the actual peak, at any rate a year of noteworthy abundance. It would appear possible therefore that regular fluctuations in numbers occur in the wheat blossom midges and that such cycles have their peaks about every fourth, fifth or sixth year. At present this is only an hypothesis and the study will have to be continued over a much longer period of years.

H. F. BARNES.

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ORIENTATION OF THE NESTS OF *FORMICA TRUNCORUM* F.
IN NORTH NORWAY.

THE photograph (Pl. X) shows a large nest of this species of wood ant, which is similar in general appearance and habits to the common *Formica rufa*, but has the habit of heaping up its nesting material against the south side of the tree stumps by which it lives. Only one nest was seen in the pine-woods, but half-a-dozen occurred in the hay meadows with their scattered birch trees



Photo. C. Elton

Nest of Wood Ant (*Formica truncorum*) on south side of pine stump in pine wood at Punta, Reisen Valley, Troms, Norway, in August 1930.

ELTON—ANTS IN NORTH NORWAY

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which give an orchard-like impression to the scenery. Here the nests are made against old birch stumps, but always against the south side only. The photograph was taken at Punta, Reisen Valley, North Norway, during the Oxford University Lapland Expedition, in August, 1930, and the specimens are deposited in the Hope Department Collection at Oxford. I have to thank Prof. E. B. Poulton, F.R.S. for kindly distributing the collections, Mr H. Donisthorpe for naming the ants, and Mr Einar Gjetmundsen, the owner of this Punta estate, for hospitality and field guidance.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

Note. The entomological journals have been abstracted by H. F. Barnes and B. M. Hobby.

1. GENERAL PAPERS ON PARTICULAR ANIMALS.

- 40. Andrews, H. W. (1931).** "British dipterological literature." Ent. Rec. 43, Supplement, 1-7.

This is an annotated list of systematic monographs and books, published in English, dealing with British Diptera.

- 41. Moseley, M. E. (1932).** "A revision of the European species of the genus *Leuctra* (Plecoptera)." Ann. and Mag. Nat. Hist. 10, 1-41.

A useful co-ordination of the scattered literature on the systematics of this group of stone-flies (known to trout fishermen as "needle-flies").

- 42. Morley, Claude (1931-2).** "A synopsis of the British Hymenopterous family Cynipidae." Entom. 1931, 150, 183, 206, 248; 1932, 15, 38, 63, 89, 108, 130-3.

2. ECOLOGICAL SURVEYS AND HABITAT NOTES.

(a) MARINE.

- 43. Ellis, A. E. (1932).** "The habitats of Hydrobiidae in the Adur Estuary." Proc. Malacolog. Soc. 20, 11-18.

A survey of the ecological distribution of three gastropods *Peringia (Paludestrina) ulvae*, *Hydrobia (Paludestrina) ventrosa*, and *H. jenkinsi*. The former are estuarine species, the last estuarine but also has been spreading into many fresh-water habitats in recent years. Notes on temperature, salinity, pH, and the plant and animal associates of various habitats were made. The three species occurred along a gradient of salinity: *H. ventrosa* in practically pure marine conditions, *P. ulvae* in widely ranging conditions of salinity, and *H. jenkinsi* in slightly brackish and fresh water. The species did not occur together in this area.

- 44. Alexander, W. B. (1932).** "The natural history of the Firth of Tay." Trans. and Proc. Perthshire Soc. Nat. Sci. 9, 35-42.

This survey formed part of a scheme of investigation on pollution of rivers and estuaries. Thirteen stations were studied, all between high and low tide, and partly by shore-collecting, partly by dredging during high tide. The species are listed, and these include the birds observed.

- 45. Fraser, J. H. (1932).** "Observations on the fauna and constituents of an estuarine mud in a polluted area." J. Marine Biol. Ass. 18, 69-85.

A study of intertidal mud in the upper part of the Mersey estuary. Species in various accurately defined habitats are listed. *Mya arenaria* was associated with presence of stones, while *Macoma balthica* was particularly abundant in thick mud.

(b) FRESHWATER.

- 46. Akehurst, S. C. (1931).** "Observations on pond life, with special reference to the possible causation of swarming of phytoplankton." J. Roy. Micr. Soc. 52, 237-65.

A great deal of information—quantitative monthly records of plankton, etc.—is contained in this paper, which does not lend itself to summary, owing to the large amount of speculation interspersed with the facts. The theories and the facts are both of interest, and contain many scattered notes on plankton animals, as well as on phytoplankton. Several ponds are described in some detail.

- 47. Hindle, E. (1932).** "Some new thermophilic organisms." *J. Roy. Micr. Soc.* 52, 123-33.

Some organic scum from the surface of a hot spring (54° C.) at Dax near Bordeaux, was brought home and cultured. Amoebae and spirochaetes were obtained and their temperature reactions studied. An amoeba (? *Hartmannella* sp.) lived well in culture at 54° C., though not at 37° C. (blood heat): but cysts survived 0°-60° C. These records disprove the usual idea that all amoebae and spirochaetes are very susceptible to high temperatures. In these instances the optimum temperature was very far above blood heat. There is a fascinating summary of other published work on this subject.

- 48. Ellis, A. E. (1931).** "Notes on some Norfolk Mollusca." *J. Conch.* 19, 177-8.

The plant and mollusc associations of two aquatic habitats; and the slugs from certain woods where *Arion subfuscus* occurs, together with notes on plants, and the fungi which the slugs eat.

- 49. Clarke, W. J. (1931).** "Distribution of the crayfish (*Astacus pallipes*) in Yorkshire." *Naturalist*, 30.

Records occurrence in waters connected with the Derwent, and in trout stomachs from this area.

- 50. Smith, S. H. (1932).** "Crayfish (*Astacus pallipes*) in Yorkshire, 1931." *Naturalist*, 78.

Notes on occurrence in certain rivers and lakes. Evidence of occasional sudden decrease in certain areas.

W. E. L. Wattam (*Naturalist*, 1931, 93) records crayfish from whole of Leeds and Liverpool Canal between Huddersfield and Marsden, also in Ribble at Horton-in-Ribblesdale), while **J. W. Dent** records it from River Nidd tributary 25 years ago.

- 51. Balfour-Browne, F. (1932).** "The aquatic Coleoptera of the Scilly Islands, with some remarks upon the genus *Philhydrus* and upon 'composite species.'" *Ent. Mo. Mag.* 68, 89-104.

- 52. Donisthorpe, H. (1931).** "Coleoptera, etc., in moorhens' and swans' nests." *Ent. Rec.* 43, 177.

In addition to beetles, the Trichopteron *Cyrnus trimaculatus* and the Hemipteron *Ischnodemus sabuleti* occurred in the nests.

- 53. Tottenham, C. E. (1932).** "A few days among the water-beetles of mid-Perthshire." *Ent. Mo. Mag.* 68, 45-50.

Collecting notes from large lochs, rivers and streams and small mossy or grassy pools and bogs.

- 54. Karandikar, K. R. (1931).** "The early stages and bionomics of *Trichocera maculipennis* (Meig.) (Diptera, Tipulidae)." *Trans. Ent. Soc. Lond.* 79, 249-60.

This Tipulid breeds in the filters of a distillery plant.

(c) LAND.

See also 48.

- 55. O'Mahony, E. (1931).** "Notes on the mammals of the North Bull, Dublin Bay." *Irish Nat. J.* 3, 199-201.

On this island, which is mainly covered with sand-dunes, there are a few hares and rabbits, many mice, and some brown rats. The mice are *Apodemus sylvaticus*, here living in the open and making deep burrows (one was 5 ft. deep); in one instance they had collected dandelion seeds in heaps for food. The house mouse was formerly stated to occur wild, but does not now.

- 56. Longbottom, M. (1931).** "Bird ecology of field and hedgerow." North-Western Nat. 6, 139-55.

An exact study of the bird population of a hawthorn hedge (with some oak trees) in pasture fields in Airedale. A map of nests is given, and lists of the resident and visiting species. A useful contribution towards a general survey of animal communities in England.

- 57. Oldham, C. (1932).** "Altitudinal range of the lesser whitethroat (*Sylvia curruca*)."
Ibis, 162-3.

This species is in Britain a characteristic lowland bird, below 1000 ft. It was found at 4500-7500 ft. in the Swiss Alps, in pine forests, associated with crossbills, nutcrackers, crested tits, etc., and occasionally observed higher up still; but it did not usually go above the tree limit.

- 58. Bristowe, W. S. (1931).** "The spiders of the Farne Islands." Proc. Zool. Soc. London, 1383-85.

Lists of species, together with some general notes on the island environments, and lists of some of the plant species. The islands are inhabited by many sea birds.

- 59. Womersley, H. (1932).** "A short account of the Collembola and Thysanura of Epping Forest." Essex Nat. 23, 116-20.

Contains general habitat notes for each species.

- 60. Newman, L. H. (1931).** "Sark Lepidoptera." Ent. Rec. 43, 184-6.

This paper deals with butterflies only. There is a complete absence of the Hesperiidae and the "fritillaries" and "blues" are not well represented. Such butterflies as *Euchloë cardamines*, *Limenitis sibilla* and *Aphantopus hyperantus*, which are comparatively common in the British Isles, are quite unknown in the Channel Islands. An account is given of a strong migration of *Pieris brassicae* and a weaker one of *Colias croceus*. Circumstantial evidence suggests that *Pieris rapae*, *Pyrameis cardui*, and *Pyrameis atlanta* were migrating at the same time.

- 61. Donisthorpe, H. (1932).** "Insects inhabiting a fungus-attacked mountain ash." Ent. Mo. Mag. 68, 14-15.

List includes the "furniture beetle" *Anobium domesticum*, a Microlepidopteron; and the Crabronids, *Pemphredon lugubris* Latr. and *Crabro chrysostomus*; the cells of the latter packed with the flies *Lagopticus* sp. (*pyrastis* L.?) and *Eristalis arbustorum*.

- 62. Fordham, W. J. (1932).** "Flies of the genus *Chilosia*, Meigen, in East Yorkshire." Naturalist, 81-5.

A list of species of these hover-flies giving localities in Yorkshire and summary of distribution in other parts of Britain and abroad, and date of appearance and disappearance, together with certain habitat notes, e.g. flowers visited by adults.

- 63. Poulton, E. B. (1931).** "Diptera (Milichiidae) bred from the nest of the bee *Anthophora pilipes* F., by A. H. Hamm." Proc. Ent. Soc. Lond. 6, 81-2.

Records about a dozen larvae of *Cacoxenus indagator* from nest of Mason bee.

- 64. Taylor, E. (1931).** "On the pupation of *Cylindrotoma distinctissima* Meig., a Tipulid infesting *Caltha palustris* L." North Western Nat. 6, 17-18.

- 65. Donisthorpe, H. (1931).** "Coleoptera found in a 'birch-bracket' fungus, *Polyporus betulinus*." Ent. Rec. 43, 14.

- 66. Donisthorpe, H. (1931).** "Teredus nitidus F., in company with ants." Ent. Rec. 43, 141-2.

"As to whether *Teredus* is really a myrmecophilus beetle I have my doubts; nevertheless I find on looking up my various captures of this insect in Windsor Forest that on every occasion, where more than one specimen was taken, the same tree was inhabited by the ant *A. (D. brunneus)*."

- 67. Donisthorpe, H. (1931).** "Myrmecophilous notes from Monmouthshire." Ent. Rec. 43, 125.

Six species of beetles and one larva of a bug found in a nest of *Formica rufa*. The beetle *Dinardia dentata* was plentiful in the nests of *Formica sanguinea*.

- 68. Blair, K. G. (1931).** "The beetles of the Scilly Islands." Proc. Zool. Soc. London, 1211-58.

574 species are listed in twenty pages of tables giving the distribution within the Scilly Islands, by islands and rough general habitats, also occurrence on Lundy and parts of the adjacent mainland. The composition of the beetle fauna is discussed. The author concludes that there are probably no endemic forms.

- 69. Donisthorpe, H. (1931).** "A curious aphid." Ent. Rec. 43, 116-17.

The author records the results of sweeping in the evening in a plantation in Windsor Forest, on high sandy ground, consisting of birch, oak, and Scots pine, and fairly long grass and herbage beneath. An aphid and about 130 species of beetles belonging to 11 different families were taken and are recorded.

- 70. Butterfield, R. and Fordham, W. J. (1931).** "Aculeate Hymenoptera of Yorkshire." Naturalist, 155-8.

This section includes notes on distribution, activity, food, habits, etc., of Trypoxylonidae, Mellinidae, Nyssonidae, Oxybelidae, and Crabronidae.

- 71. Nixon, G. E. J. (1931).** "A new British Proctotrupid of the sub-family Belytinae." Ent. Rec. 43, 83-4.

Brunnicophilus donisthorpei (new genus and species) was found in nests of the ant *Acanthomyops brunneus*.

- 72. Marriner, T. F. (1931).** "The Cumberland Aleurodes." Ent. Rec. 43, 21-3.

Distribution of this Hemipterous genus in Cumberland and host plants on which they are found.

- 73. Harrison, J. W. (1931).** "Some observations on Aleurodidae." Ent. Rec. 43, 84-5.

Records of distribution and food plants. Includes comments on paper of **T. F. Marriner (72)**.

- 74. Tattersall, W. M. (1931).** "A terrestrial amphipod new to the fauna of Lancashire and Cheshire." North Western Nat. 6, 224-5.

Talitrus alluaudi is a tropical crustacean closely allied to the common sandhopper of British shores. It has established itself in hothouses in Europe and recently also in Ohio. A second species occurs in hothouses at Kew, while a third lives out-of-doors on the Scilly Islands.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See also 46, 47, 138, 144.

- 75. Abbot, W. M. (1931).** "Rook versus starling." Irish Nat. J. 3, 191-2.

A starling flock tried unsuccessfully to drive rooks from their roosting site.

- 76. Rowberry, E. C. and Ferrier, J. M. (1931).** "Carrion crow attacking squirrels." British Birds, 25, 129-30.

Two independent records, one instance being of a grey squirrel, the other a squirrel unspecified.

- 77. Flintoff, R. J. (1931).** "Bees and birds." Naturalist, 350.

Records jackdaws nesting in hole in tree occupied also by a swarm of hive bees.

78. Oldham, C. (1931). "Spawning season of the common toad." *Naturalist*, 143.

Spawning at end of February, 1931, in west Cornwall.

79. Bhatia, D. (1932). "Factors involved in the production of annual zones on the scales of the rainbow trout (*Salmo irideus*)."*J. Exp. Biol.* 9, 6-11.

Experiments proved that the size of the rings of growth on the scales could be entirely controlled by varying the amount of food, but were not affected by temperature. Periodic zoning similar to that found in winter and summer scale-growth was produced artificially.

80. Boycott, A. E., Oldham, C. and Waterston, A. R. (1932). "Notes on the lake *Lymnaea* of south-west Ireland."*Proc. Malacolog. Soc.* 20, 105-27.

The mountain loughs in this region are rather barren and characterised by sparse phanerogamic vegetation, in which *Lobelia dortmanna* is characteristic, while the only molluscs besides *Lymnaea* are *Ancylus fluviatilis* and *Pisidium*. In these upland lakes occur curious thin-shelled *Lymnaeas* which are probably in part phenotypic forms of the common *L. peregra* found in the lower lakes. The fact that each lake has only one of the many varieties of shell-sculpture that are found points to the existence also of local genotypic races. The snails are now being investigated experimentally. The two described species *L. involuta* and *L. praetenuis* really grade through a series of forms, but never in the same lake.

81. Clarke, G. L. (1932). "Quantitative aspects of the change of phototropic sign in *Daphnia*."*J. Exp. Biol.* 9, 180-211.

The author was searching for a complete mechanical-physiological explanation of the varying responses of *D. magna* to light, and carried out ingenious experiments which showed that the type of wandering of individuals in a beam of light was partly dependent upon their age, also upon the conditions of the medium, but not on the intensity of the light. He believes that these results are consistent with the hypothesis that change of response to light is based upon a reversible chemical reaction.

82. Imms, A. D. (1932). "Temperature and humidity in relation to problems of insect control."*Ann. Appl. Biol.* 19, 125-43.

Summary of recent experimental studies of these two factors in relation to applied entomology.

83. Buxton, P. A. (1931). "The law governing the loss of water from an insect."*Proc. Ent. Soc. London*, 6, 27-31.

"Assuming that saturation deficiency can be applied to insects in general, and this assumption appears probable, it follows that we can compare two places or two seasons and say that they are identical or not in saturation deficiency, that is to say in the amount of loss of water that would take place from an insect. The use of this law may lead to great advances in the understanding of the relation between living insects and the environments in which they live."

84. Uvarov, B. P. (1931). "Insects and climate."*Trans. Ent. Soc. London*, 79, 1-247.

One of the most important papers of the year. The author gives bibliographical references to over 1150 papers and books and summarises these under the following headings: Part I. The Physical factors of insect life: 1, Heat; 2, Humidity; 3, Other climatic factors; 4, Combination of several factors. Part II. Weather, climate and insects: 5, Relation of weather to the activities of insects; 6, Daily and annual cycles; 7, Climate and distribution; 8, Effect of climate on abundance; 9, Climate and weather in economic entomology. There are excellent indices to authors and to subjects.

85. Mellanby, K. (1932). "The influence of atmospheric humidity on the thermal death point of a number of insects."*J. Exp. Biol.* 9, 222-31.

A technique for keeping small insects under conditions of high temperature and controlled humidity is described. The rat flea (*Xenopsylla cheopis*), human louse (*Pediculus humanus corporis*), blow-fly (*Lucilia sericata*), and meal-worm (*Tenebrio molitor*) were used. Relative humidity does

not influence thermal death-point after only an hour's exposure, but does so markedly after 24 hours' exposure. This is attributed to drying up, and was less marked in larger than smaller insects. The rat flea showed the following changes of thermal death-point. R.H. 0, T.D.P. 22° C.; R.H. 30, T.D.P. 27° C.; R.H. 60, T.D.P. 32° C.; R.H. 90, T.D.P. 36° C.

86. Brown, J. M. (1931). "Late and early stone-flies in North Derbyshire." *Naturalist*, 110.
87. Atkins, W. R. G. (1932). "Nitrate in sea water and its estimation by means of diphenylbenzidine." *J. Marine Biol. Ass.* 18, 167-92.

4. PARASITES OF ANIMALS.

See also 61, 63, 113.

88. Petch, T. (1932). "British species of *Hirsutella*." *Naturalist*, 45-9.
Descriptions of two species of fungi which are parasitic on beetles and caterpillars respectively.
89. Petch, T. (1931). "*Isaria arachnophila* Ditmar." *Naturalist*, 247-50.
A very useful summary of information (with literature references) about this fungus, which occurs on spiders, and is now known as *Gibellula aranearum*. There is another genus *Hymenostilbe* which has in the past been confused with *Gibellula*.
90. Haines, F. H. (1932). "A Syrphid fly killed by a fungus." *Entom.* 65, 114-15.
Melanostoma scalare killed by an *Empusa*. Notes of other records of flies killed by an *Empusa*, which may well be an *Entomophthora*, are added by F. W. Edwards.
91. Cameron, T. W. M. (1932). "Some notes on the parasitic worms of the Scottish red deer." *Proc. Roy. Physical Soc. Edinburgh*, 22, 91-7.
Lists the parasites and discusses possible methods of controlling worm infestation in wild deer. Two are suggested: first, keeping down the density of deer by killing, and secondly the use of "anthelminthic and tonic licks, a method still in the experimental stage, but one which seems to hold considerable promise of success."
92. Imperial Bureau of Agricultural Parasitology (1931). "Hand-list of helminth parasites of the rabbit." *J. Helminth.* 9, 105-16.
Refers to the wild rabbit, *Oryctolagus cuniculus*. Full references to literature.
93. Oldham, J. N. (1931). "The helminth parasites of common rats." *J. Helminth.* 9, 49-90.
List of worms recorded from rats in all parts of the world, with full bibliography.
94. Cameron, T. W. M. (1932). "On a new species of Oxyurid from the grey squirrel in Scotland." *J. Helminth.* 10, 29-32.
A nematode *Enterobius sciuri* from a specimen in the north of Scotland.
95. Robertson, D. (1932). "Wood pigeon infested with cestodes." *Scottish Nat.* 52.
The tapeworm *Skrjabina columbae*.
96. Morgan, D. O. (1931). "On the occurrence of gapeworms in nestling starlings and adult fowls." *J. Helminth.* 9, 117-20.
Records that a nestling starling free from outside contact except by parents bringing food, contained *Syngamus trachea*, probably derived from earthworms used as food. Reviews evidence about starlings as reservoir of "gapes," and concludes that they are probably important, though there is evidence that they carry a mild physiological strain.

- 97. Rees, F. G. (1932).** "An investigation into the occurrence, structure, and life-histories of the Trematode parasites of four species of *Lymnaea* (*L. truncatula* (Müll.), *L. peregrina* (Müll.), *L. palustris* (Müll.), and *L. stagnalis* (Linne)), and *Hydrobia jenkinsi* (Smith) in Glamorgan and Monmouth." *Proc. Zool. Soc. London*, 1-32.

The title is almost a summary in itself. Ten species of larval flukes were identified in the four species of *Lymnaea*, all being specific to one host only. It is pointed out that the liver-fluke occurs in parts of the world where its usual host *L. truncatula* is absent, and in these regions lives in other snails. It was not found in the other four species in South Wales. 729 specimens of *Hydrobia* (*Paludicrina*) examined had no trematode parasites, and none are known from this species, which has invaded freshwater streams in recent decades, and is now widespread in Glamorgan and Monmouth.

- 98. Cameron, A. E. (1932).** "Arthropod parasites of the red deer (*Cervus elephas* L.) in Scotland." *Proc. Roy. Physical Soc. Edinburgh*, 22, 81-9.

Results of two years investigation in Perthshire. Deer have increased in numbers. The theory that they carry the warble-fly of cattle is disposed of. Five parasites were found: a tick, a warble-fly, an Oestrid nostril-fly, a Hippoboscid fly, and a biting louse.

- 99. Hobby, B. M. (1931).** "The Sphecid wasp *Mimesa (Psen) bicolor* Jur. capturing parasitised Jassid prey." *Proc. Ent. Soc. London*, 6, 11.

Two species (*Paramesus nervosus* and *Athyranus sejungendus*) were observed as prey, the former was unparasitised but of the latter 10 (74 per cent.) were parasitised by Dryinid larvae.

- 100. Poulton, E. B. (1931).** "Observations by Oswald H. Latter on the insect enemies of the British bee, *Osmia rufa* L." *Proc. Ent. Soc. London*, 6, 81.

Only one male and one female emerged from nineteen cells constructed in a window frame. From the remaining cells were bred nineteen Milichiid flies (*Cacoxenus indigator*) and two beetles (*Megatoma undata*).

- 101. Donisthorpe, H. (1931).** "Tetrastichus miser Nees...a Chalcid parasite on species of *Cassida*." *Ent. Rec.* 43, 70.

This Chalcid has been bred from pupae of *Cassida nebulosa* and also from *C. rubiginosa*.

- 102. Blair, K. G. (1932).** "Some notes on the galls of *Lipara lucens* Mg." *Ent. Mo. Mag.* 68, 10-13.

Contains notes on the parasites of this species.

- 103. Renouf, L. P. W. (1932).** "Xantho incisus Leach and *Cancer pagurus* L. infested with *Sacculina carcinii* Thompson, on the south coast of Co. Cork." *Ann. and Mag. Nat. Hist.* 10, 132-3.

The shore crab (*Carcinus moenas*) is rare in this area and the parasitic cirrihipe usually associated with it was found on two other species. Notes on other ectoparasites of the edible crab (*Cancer*) are also given.

- 104. Renouf, L. P. W. (1932).** "Mollusc galls on *Ascidia aspersa* (O. F. Muller)." *Ann. and Mag. Nat. Hist.* 10, 114-15.

The lamellibranch mollusc *Musculus* (*Modiolaria marmorata*) is a common parasite inside sea-squirts (Ascidians) in the Lough Ine area in southern Ireland, but seldom causes reaction in host tissues. Two examples of galls contained *Musculus*, while one also had *Hiatella (Saxicava) arctica*, another lamellibranch.

5. PLANT-GALLS AND POLLINATION.

(a) PLANT-GALLS.

See also 130.

- 105. Bagnall, R. S. (1932).** "The gall-midges (Cecidomyidae) of the aspen (*Populus tremula*) in Scotland, with description of a new *Harmandia* gall." *Scottish Nat.* 73-6.

Contains a key to British gall-midges found on aspen.

- 106. Bagnall, R. S. (1932).** "A preliminary account of the Scottish gall midges." *Scottish Nat.* 77-88 and 109-21.

A large mass of data relating to host-plants, places and dates of discovery.

- 107. Burkhill, H. J. (1931).** "*Oligotrophus ventriculus* Rubs. etc." *Naturalist*, 285-6.

Points out various records additional to those contained in Swanton's book on galls, and in addition to quoted references some original records of gall-midges and their host plants.

- 108. Barnes, H. F. (1932).** "On the gall midges injurious to the cultivation of willows. I. The bat willow gall midge (*Phabdophaga terminalis* H. Lw.)." *Ann. Appl. Biol.* 19, 243-52.

Experiments showed that this midge has a definite host-plant preference choosing bat willow (*S. coerulea*) if possible. While also breeding on golden willow (*S. alba* var. *vitellina*), it will not attack varieties of *S. triandra*, *S. viminalis* and *S. purpurea*. Alternate forms of gall are described and figured.

- 109. Bagnall, R. S. (1932).** "On the Scottish species of gall wasp that affect the Compositae." *Scottish Nat.* 21-3.

Lists ten species and their hosts.

- 110. Goodey, T. (1931).** "New hosts of *Anguillulina dipsaci* (Kühn, 1858) Gerv. and V. Ben. 1859, with some notes and observations on the biology of the parasite." *J. Helminth.* 9, 191-6.

(b) POLLINATION.

See also 62.

- 111. Richards, O. W. (1931).** "Insects fertilising *Orchis maculata* L. near Oxford." *Proc. Ent. Soc. London*, 6, 59.

Records *Empis livida*, *Apis mellifica*, *Bombus pratorum*, *Poitherus sylvestris*, *Augiades zyganeus* and *Grammoptera ruficornis* on the flowers. *Poitherus sylvestris* and *Angitia rufipes* were caught bearing pollinia (probably of this species of Orchid).

- 112. Poulton, E. B. (1931).** "Insect carriers of Orchid pollinia, collected by Col. M. J. Godfrey." *Proc. Ent. Soc. London*, 6, 70.

Records *Empis tessellata* on *Orchis elodes*; *Apis mellifica* on *Himantoglossum hircinum*; *Halictus leucozonius* on *Orchis maculata*; *Dolerus picipes* on *Cephalanthera ensifolia*.

6. FOOD-HABITS.

See also 48, 49, 55, 108, 130, 132, 140.

- 113. Mason, F. A. (1931).** "Fungi." *Naturalist*, 27-8.

Red squirrel eating *Boletus elegans* (it was already known to eat seven other species of *Boletus*). Large numbers of dead froghoppers (*Philaenus spumarius*) attacked by fungus *Entomophthora sphaerosperma*.

- 114. Charteris, G. (1931).** "A pertinaceous pied wagtail and a grey squirrel." *British Birds*, 25, 130.

A pied wagtail made five successive nests, involving the laying of about twenty eggs, and all were destroyed by various factors, the last being a grey squirrel which killed the nestlings.

- 115. Lawson, A. K. (1932).** "Mollusca eaten by rabbits." *J. Conch.* 19, 190. *Helix nemoralis* and *H. aspersa*.

- 116. Poulton, E. B. (1931).** "British moths eaten by bats." *Proc. Ent. Soc. London*, 6, 18.

- 117. Poulton, E. B. (1931).** "Further observations on the common earwig (*Forficula auricularia* L.) as the prey of the long-eared bat (*Plecotus auritus* L.). Convincing evidence of the nocturnal flight of *F. auricularia*." *Proc. Ent. Soc. London*, 6, 93-4.

Records forceps of *F. auricularia* among débris dropped by bats. Also wings of Noctuid moths *Taeniocampa gothica* and *T. instabilis*. The large numbers of earwigs which suddenly appeared in tents could only be explained by flight from a wide area probably stimulated by the scent of food.

- 118. Moffat, C. B. (1931).** "The long-eared bat." *Irish Nat. J.* 3, 182-5.
Includes notes on habits and food (Lepidoptera).

- 119. Poulton, E. B. (1931).** "Swallows capturing *Polyommatus corydon* Poda, on the wing, near Painswick." *Proc. Ent. Soc. London*, 6, 2-3.

Other papers, bringing forward evidence (e.g. beak-marks on wing) that birds attack Lepidoptera are: *ibid.* 3, 16-17, 18, 90, 91.

- 120. Flintoff, R. J. (1931).** "Starlings, rooks, and caterpillars." *Naturalist*, 334.

The birds were flocking to eat oak-moth caterpillars, possibly *Tortrix viridana*.

- 121. Owen, J. H. (1931).** "The feeding habits of the sparrowhawk." *British Birds*, 25, 151-5.

A great variety of small mammals and birds are listed.

- 122. Leach, E. P. (1931).** "Ringed birds in pellets and nests of owls and hawks." *British Birds*, 24, 292-5.

Food records for little owl, tawny owl, peregrine falcon, kestrel, sparrowhawk. These include birds, mammals, and frogs. Records named beetle and moth from little owl's nest.

- 123. Allen, F. (1931).** "Unusual behaviour of linnets." *Naturalist*, 79.

Flocks of linnets feeding on pupae of *Oligotrophus ventriculus* in the stem-bases of *Molinia caerulea* on tops of hills. Notes that some other birds, e.g. starlings feed also on this insect in winter.

- 124. Clarke, W. J. (1931).** "Food of the codfish." *Naturalist*, 144.

Stomach of one from Scarborough contained three species of crab, *Stenorhynchus tenuirostris* *Inachus dorsettensis*, and *Hyas coarctatus*, as well as a dragonet (*Callionymus lyra*), and prawns.

- 125. Steven, G. A. (1932).** "Rays and skates of Devon and Cornwall.

2. A study of the fishery; with notes on the occurrence, migrations and habits of the species." *J. Marine Biol. Ass.* 18, 1-34.

A careful study which refers especially to *Raja clavata*, but also to other species. Rays and skates have become during the twentieth century an important item in British fisheries. Much remains to be found out about their movements. The number caught has declined during the last five years, and this probably represents a real decrease in nature. Young rays eat mainly small Crustacea (Amphipoda and Crangonids); later they eat larger Crustacea such as crabs. *R. clavata* was found to eat many herring and sprats at times, while the large *R. batis* includes other species of rays in its diet.

- 126. Laing, F. (1932).** "*Borkhausenia pseudospretella* and other house moths."

Ent. Mo. Mag. 68, 77-80.

Notes on feeding habits. Further reference in *J. C. F. Fryer (ibid.* 137-8).

- 127. Edwards, F. W. (1932).** "Notes on Highland Diptera, with descriptions of six new species." *Scottish Nat.* 43-52.

Includes some habitat notes, e.g. height records of Tipulids, and the preys of *Empis lucida*.

- 128. Hobby, B. M. (1931).** "The prey of *Coenosia tigrina* F., and other species of the genus." *Proc. Ent. Soc. London*, 6, 13-15.

Other papers on predaceous insects by the same author are: *ibid.* 16, 47-9, 67-8, 75, 87-8.

- 129. Edwards, F. W. (1932).** "A midge attacking lace-wing flies in Britain."

Ent. Mo. Mag. 68, 114-15.

Forcipomyia eques recorded as attacking *Chrysopa flavifrons* and *C. perla*. This midge sucks the veins of the wings. The only previous British record was of *F. papilionivora* on the wings of a "Cabbage White" butterfly.

7. THE NUMBERS OF ANIMALS.

See also 50, 56, 84, 91, 114, 125.

- 130. Bramley, W. G. (1931).** "Mammals, amphibians, reptiles, and fish."

Naturalist, 13-14.

Scattered notes on abundance of mice, squirrels, otters, badgers, bats, seals, etc. in 1930. Grey squirrels were increasing and spreading. Seen opening oak galls, and eating young hazel nuts. Notes reduction of numbers of frogs through previous drought affecting spawn. Notes on fish include statement that salmon season was very poor, while floods affected fish life in many ways.

- 131. Macintyre, D. (1932).** "Arctic hares in Scotland: amazing increase within living memory." *Field*, February, 223.

Refers to spread and increase of the alpine hare in the south of Scotland and the damage they are supposed to do to sheep country.

- 132. Beveridge, G. (1932).** "The introduction of the rabbit to the isle of Vallay, North Uist." *Scottish Nat.* 33-4.

There were none in 1900, one pair in 1905 (method of introduction unknown), nearly 1000 shot in 1916, and over 2000 in 1927. They cause additional wind erosion of the sandy soil, through their burrowing. They eat seaweed at certain seasons.

- 133. Parnell, I. W. (1932).** "Some notes on the natural history of the Scottish red deer." *Proc. Roy. Physical Soc. Edinburgh*, 22, 75-80.

An interesting general account of history, habits, changes in numbers and size, with little or no fresh matter.

134. Local Reports on Birds.

In *British Birds*, 1932, 25, 233-6, a number of local and county papers on bird status, numbers, distribution, etc. are reviewed or summarised. These include the reports of Oxford Ornithological Society, Cambridge Bird Club, Norfolk and Norwich Naturalists' Society, London Natural History Society, Cardiff Naturalists' Society, Marlborough College Natural History Society, and Eton College Natural History Society, also from Somerset and Wiltshire (no reference given). These reports cannot possibly be abstracted and much of the information is of local interest, or awaits co-ordination into regional summaries.

- 135. Smalley, F. W. (1932).** "Changes in the distribution of British Geese." *Scottish Nat.* 67-72.

- 136. Harrisson, T. H. (1932).** "The birds of Lundy Island from 1922 to 1931, with special reference to numerical fluctuations." *British Birds*, 25, 212-19.
Records increase in some and decrease in others.

- 137. Moffat, C. B. (1931).** "A remarkable wagtail roost." *Irish Nat. J.* 3, 206-8.

Pied wagtails occupied a tree-roost right in the middle of Dublin. The numbers were estimated at 600. There is a flashlight photograph of the roosting birds.

- 138. Wynne-Edwards, V. C. (1931).** "The behaviour of starlings in winter." *British Birds*, 24, 346-53.

A study of roosts in the Bristol district. Notes two instances of redwings being driven from roosts by starling flocks. Roosts are often shifted during the winter. Probably the feeding flocks roost as independent units. In one case these used to arrive at different times, and the author believes that the flocks represent different ages and states of the reproductive organs and that they react differently to light intensities. The evidence for these beliefs is to be published later.

- 139. Dallman, A. A. (1932).** "A great Shropshire starling roost." *North-Western Nat.* 7, 126-7.

A historical note on a roost at Petton in 1909.

- 140. Nethersole-Thompson, D. (1931).** "The field habits and nesting of the hobby." *British Birds*, 25, 142-50.

Includes notes on the food—both insects and various small birds, in some areas chiefly larks and pipits. Also account of the breeding habitats. This hawk is decreasing. The merlin and hobby do not appear to overlap in their British distribution.

- 141. Nicholson, E. M. (1931).** "Supplementary notes on the 'British Birds' census of heronries." *British Birds*, 25, 159-61.

- 142. Lack, D. L. (1932).** "Some breeding-habits of the European nightjar." *Ibis*, 266-84.

A study of the breeding biology of a nightjar population on an area of sandy heath in Norfolk. There was about one pair of birds to every 17-20 acres. It was shown that singing males could be used as an index of the population. Nest territories were rather evenly spaced, but the birds did not show strict confinement to food territories. The author points out that the birds showed every sign of being "territorial" birds, yet did not act as though compelled to be so by "economic" reasons. A large amount of visiting took place between neighbouring pairs.

- 143. Hurrell, H. G. (1931).** "Numerical status of great black-backed gull in Devon." British Birds, 25, 136-8.

Great decrease.

- 144. Robinson, H. W. (1931).** "Mortality among young common terns." British Birds, 25, 135-6.

Records 4-5 per cent. mortality in very hot weather, and about 3 per cent. in cold wet weather. The basis of the figures is not quite clear.

- 145. Imperial Bureau of Agricultural Parasitology (1931).** "On the eel-worm *Heterodera schachtii* as a potential danger to the sugar-beet industry in Britain." J. Helminth. 9, 97-104.

- 146. Scott, H. (1932).** "Swarming of a Harpaline beetle." Ent. Mo. Mag. 68, 13-14.

Note on the swarming of *Pseudophonus griseus* in very large numbers in France. Further reference to swarming of beetles are given.

- 147. Stephen, A. C. (1932).** "Notes on the biology of some lamellibranchs in the Clyde area." J. Marine Biol. Ass. 18, 51-68.

It is now widely believed that marine fish fluctuations are mainly caused by good and bad survival years for the young fry. This conclusion is here applied tentatively to certain bivalve molluscs (the species studied were *Cardium edule*, *Tellina tenuis*, *T. fabula*, and *Abra abra*). Good spat survival years were found to occur at intervals, and may coincide with clearing of the ground by mortality of the old specimens.

8. MIGRATION AND DISPERSAL.

See also 97, 125.

- 148. M'Naughton, J. (1931).** "Musquash or musk-rat (*Fiber zibethicus*) in Strathallan." Trans. Stirling Nat. Hist. and Arch. Soc. 1930-1, 152-3.

A pair escaped in 1928 from a fur-farm, established themselves in a swamp, and increased. Sixteen houses were counted on one area. The banks of the Allan and Carsebreck Loch have been damaged badly by burrowing. Further notes (*ibid.* (1931-2), 178-80) state that the muskrats have advanced into the Forth Valley near the Bannock burn. There are notes on muskrat habits and also upon the occurrence of grey squirrel at Blair Drummond.

- 149. Middleton, A. D. (1931).** "Muskrats in Great Britain: a new danger to the country." Field, August, 319.

A short note on the escape and spreading of muskrats in British waters. The damage done in Europe by the burrowing into and undermining of banks is considerable, leading to floods and the destruction of canals and waterworks. The importance of preventing such damage in this country is emphasised.

- 150. "Salop" (1932).** "The muskrat danger." Field, May, 688.

Describes the spread of muskrats in Shropshire and the dangers to which waters and farmland are exposed.

- 151. Leslie, J. (1931).** "Liberation of greater horseshoe bats in Co. Monaghan, and other bat notes." Irish Nat. J. 3, 222-3.

The Editor of the I.N.J. comments as follows: "We are unable to share our correspondent's hope that the bats let loose by him will breed and increase in this country, for such introductions have a very hampering effect on zoological study which concerns itself with the natural distribution of animal life....Mr Leslie is however entitled to our thanks for informing us of what he has done, as the mischief would be multiplied tenfold if the animals were introduced without public notification."

- 152. Masefield, J. R. B. (1931).** "Zoology." Trans. N. Staffs. Field Club, 45, 103-5.

Notes on the spread of the grey squirrel into Staffordshire.

- 153. Flintoff, R. J. (1931).** "The grey squirrel at Goathland, North Yorkshire." Naturalist, 44.

Notes first appearance of this species at various dates and places.

- 154. Witherby, H. F. and Leach, E. P. (1931).** "Movements of ringed birds from abroad to the British Isles and from the British Isles abroad." British Birds, 25, 110-28 and 174-92.

A very useful summary of scattered continental records as well as those obtained by the British ringing scheme. Maps are given for most species. It can be seen how the winter visiting mallard, blackbird and starlings come from the Baltic and the North Sea coast areas, while the wheatear, whinchat, pied wagtail, meadow and tree pipits, linnet, and cormorant migrate south to the western parts of France and Spain, and the swallow to South Africa.

- 155. Boyd, A. W. (1931).** "On some results of ringing greenfinches." British Birds, 24, 329-47.

Ringing nestlings and trapped birds showed that the greenfinches bred in England are comparatively sedentary in habits, most being recovered within a few miles of their centre, even in successive winters. It was proved that a fair number reached an age of three years, and one at least five and a half years.

- 156. Beeston, T. J. (1931).** "Migration routes of wood-pigeons in Worcestershire." British Birds, 24, 326-8.

Clear evidence of regular autumn migration to south-west and west, often of large flocks. British wood-pigeons have been proved to be largely resident. The significance of this regular movement in autumn is not yet known.

- 157. Berry, J. (1932).** "Birds seen in Western Caithness, autumn 1931." Scottish Nat. 39-42.

Includes three striking photographs of large flocks of migrant snow buntings.

- 158. Green, J. and Flintoff, R. J. (1931).** "Desertion of rookeries." Naturalist, 169-72 and 199-203.

Records history of several desertions and shows that they were not caused by carrion crows, as is widely believed. The relation of rook roosts to deserted rookeries is also discussed.

- 159. Charteris, G. (1931).** "Crossbills in Gloucestershire and breeding in Surrey." British Birds, 25, 22-3.

Refers to winter 1929-30. Larch and pine cones were eaten. **F. C. R. Jourdain and H. F. Witherby** (*ibid.* 25, 162 and 163) give evidence of crossbills breeding in Dorset, Hants, and Surrey.

- 160. Ritchie, J. (1932).** "Immigration of Waxwings (*Bombycilla garrulus*) in the autumn of 1931." Scottish Nat. 56.

This coincided with winds which apparently drove them out of their usual southward course from the Scandinavian area.

H. B. Booth. (*Naturalist*, 1932, 14) notes invasion in north-east England in the late autumn of 1931; **R. M. Garnett** and **G. C. Wynne** give notes (*British Birds*, 1932, 25, 223) on immigration in Norfolk and Westmorland respectively; while **J. A. S. Stendall** (*Irish Nat. J.* 1932, 4, 39) notes waxwings in Ireland. Other notes occur in the *Naturalist*, 1931, 28-30 and 56.

- 161. Bayford, E. G. (1931).** "Plague of 'lice' at Mexborough." Naturalist, 62.

Refers to unusual abundance of woodlice (*Philoscia muscorum*) which had been migrating into houses from a rubbish tip.

- 162. Laing, F. (1932).** "A note on our British domestic Psocids." Ent. Mo. Mag. 68, 68-9.

Formerly *Trogium pulsatorium* and *Liposcelis dirinatorius* were the species regularly found, with *Lachesilla pedicularia* and *Lepinotus piceus* occasionally turning up. In the post-war era *Nymphopsocus destructor* and *Myopsoecema annulata* occur almost as frequently. This change in Psocidae occurring indoors in Britain is probably due to the importation of building materials from the Continent.

- 163. Saunt, J. W. (1931).** "Some American Immigrants." Ent. Rec. 43, 11-12.

Records the introduction, in timber, of the beetles *Neoclytus erythrocephala*, *N. capra* and *Tylonotus bimaculatus*; the moth *Prionoxystus robiniae*; the bee *Xylocopa virginica* and the ants *Camponotus herculeanus*, *C. caryae*, *Pheidole megacephala* and *Cremastogaster lineolata*.

- 164. Donisthorpe, H. (1931).** "Immigrants." Ent. Rec. 43, 141.

Macroglossum stellatarum, *Pyrameis cardui* and *P. atlanta* at Putney. See also *ibid.* 126.

- 165. Tulloch, J. B. G. (1932).** "The effect of wind on butterfly migration." Entom. 65, 138-9.

Instances of whirlwinds causing dispersal of locusts and butterflies.

- 166. Lisney, A. A. (1931).** "A migration of Lepidoptera." Irish Nat. J. 3, 217.

Notes on moths and butterflies (including the painted lady butterfly, *Pyrameis cardui*). Further notes on the latter by **A. W. Stelfox**, *ibid.* 3, 232. For Channel Islands see Notice 60.

- 167. Burr, M. (1931).** "*Polygonia c-album* in Bucks." Ent. Rec. 43, 178.

- 168. Burkill, H. J. (1931).** "Are British butterflies extending their range?" Naturalist, 293-6.

Notes on fluctuations in numbers and range of various species.

- 169. Clarke, W. J. (1931).** "Locusts in North-east Yorkshire." Naturalist, 325-6.

Several records of the Migratory Locust (*Locusta migratoria*) from Yorkshire and other parts of Great Britain in 1931. This species has a very wide distribution in the Old World.

- 170. Ritchie, J. (1931).** "The great wood-wasp (*Sirex gigas*) spreads to Ross-shire." Scottish Nat. 176.

This species is apparently spreading northwards in Scotland.

- 171. Spooner, G. M. (1932).** "Notes on *Sapyga clavicornis* L." Ent. Mo. Mag. 68, 115-16.

Notes on the spread of this wasp in Cambridgeshire and Surrey. Further reference in **C. H. Mortimer** (*ibid.*).

REVIEWS

THE AUGUST ISSUE OF THE JOURNAL OF ECOLOGY (VOL. XX, NO. 2).

THE current issue of the *Journal of Ecology* contains ten papers and covers a wide range of ecological interest. No less than three papers deal with plankton and its conditions of life. Dr W. H. Pearsall of Leeds, in the second part of his contribution on Phytoplankton in the English Lakes discusses the distribution of the different types of phytoplankton in relation to the varying dissolved substances (which were the subject of the first part, published in 1930) and shows that the correlation, particularly in seasonal change, is very close. Mr R. E. Savage and Mr J. R. Lumby, of the Fisheries Laboratory at Lowestoft, respectively describe the striking influence of *Phaeocystis* on herring migrations, and the present position of our knowledge of the circulation of water in the North Atlantic and the North Sea. The latter topic, while primarily hydrographical, of course underlies the whole of the conditions of life of marine organisms, because it affects the salinity and temperature of all local waters. Both these papers are illustrated by numerous explanatory maps. Dr Nellie Carter begins a very detailed ecological study of the algal flora of two salt marshes of widely different geographical position and flora—one in the estuary of the Dovey and the other at Canvey Island in the Thames estuary. Dr W. Watson continues his extremely valuable series of papers on the Bryophytes and Lichens of different habitats: the present contribution deals with Moorland. Messrs V. C. Wynne-Edwards and T. H. Harrisson give the results of a Bird Census on Lundy Island taken in 1930. Indications of the nature of the vegetation and of the rest of the fauna are given. The outstanding difficulty in making the census was the presence of passage migrants. This paper should perhaps have appeared in the *Journal of Animal Ecology* but the authors desired it to be published in the parent periodical.

The four remaining papers deal with extra-British areas. Mr A. S. Thomas briefly discusses the Dry Season in the Gold Coast and its relation to the cultivation of Cacao. He concludes that it is the degree of dryness of the dry months (November to February), rather than that of the whole year, which is of importance as a limiting factor to the growth of Cacao. Dr E. H. Moss continues the series of papers on the Vegetation of Alberta emanating from Prof. F. J. Lewis's laboratory at the University of Alberta. This is the fourth publication in this series and deals with the Poplar consociation and related vegetation. The American aspen (*Populus tremuloides*) is the climax dominant of the drier and generally more southern areas of central Alberta, while the balsam poplar (*P. balsamifera*) is sub-climax to *Picea albertiana* in the moister, especially the northern and western, parts of the region. Messrs W. Leach and Nicholas Polunin communicate their observations on the Vegetation of Finmark (Norwegian Lapland) made on the Oxford University Exploration Club expedition in the summer of 1930. In the course of a long trek from the Porsanger Fjord to the central plateau and then down to the west coast the various altitudinal zones were traversed, from birch and local pine forest to heath and dry summit vegetation. General descriptions and lists of species are given, and also good accounts of various successions, including the conditions of vegetation on scree, which are compared with British examples. Finally Dr L. Cockayne and Mr J. W. Calder compare the vegetation of Arthur's Pass in the Southern Alps of New Zealand, as it exists to-day with its condition 34 years previously. Photographs from the same view point at the two dates are reproduced, and some valuable conclusions reached.

A. G. TANSLEY.

THE ORGANISING OF ORNITHOLOGISTS.

E. M. Nicholson. *The art of bird watching.* Pp. 1-218. Price 10s. 6d.
Witherby, London. (The Sports and Pastimes Library.)

THE triumphant success of the Heron Census of 1929, which the author and his brother, B. D. Nicholson, organised in conjunction with *British Birds*, and of its successor, the Great Crested Grebe Enquiry in 1931, under the direction of T. H. Harrisson and P. A. D. Hollom, and recently published in the same journal, have shown that there are in this country thousands of people (including many who would by no means call themselves ornithologists) who are keen to take part in organised ecological studies of wild birds. This well of enthusiasm and energy which can be tapped for any national scientific enterprise must be partly attributed to the lack of any universal or convincing point of focus for political and economic loyalties, but also the desire for more intelligent team occupations than are supplied by sports and games themselves. Those who take up the study of birds begin by learning the notes, appearance, flight and nesting habits of the usual species living in their neighbourhood. This regime provides material for some years' pleasant occupation, and with specially talented naturalists who have much time to devote to it, may be sufficient in itself. But many people soon reach a rather static position, one almost of disappointment. The watch for rarities begins—the piebald blackbird, jackdaws with malformed beaks, abnormally shaped or coloured eggs, curious nesting sites. Thus the content of most amateur ornithology of this phase partakes more of the acquisitive or possessive feeling, or of aesthetic pleasures, and seldom includes any element of constructive scientific thought. And yet, although these simple and direct pleasures are by no means to be decried (except when they masquerade under the name of science, as with "comparative oology"), there can be no doubt that the life of birds is thick with fascinating puzzles which challenge the ingenuity of the bird-watcher—if he knows what to look for.

Nicholson's book is addressed to the amateur who wants a guide to methods and aims. It is a first rate introduction to modern ideas about the ecology and life of birds. The ornithologist need no longer travel abroad for new thrills (to see new species, or to clutch new eggs), nor spend his time expanding that curious phenomenon "the British list"—curious on account of its membership rules, which, as is rumoured about some English clubs, admit members alive or dead.

Perhaps the most significant difference between this book and all previous bird books is the importance given to the map as a weapon in the study of bird ecology. A map immediately brings in the environment, and at the same time enables systematised work to be carried out; it encourages accurate objective records, and introduces naturally the concept of organised team-work over large areas. A criticism may here be made about organisation in itself: although much ecology cannot be done without it, yet Nicholson tends to adopt an attitude of worship for organisation as such (or should we say, a loathing of chaos?), and thoughts of Russia and Italy float naturally into one's mind. This is good so far as it provides leadership for what would otherwise be unharvested energy, and so far as it encourages an educational trend towards higher scientific appreciation among naturalists. But it would be bad if it stifled individual initiative or engendered an attitude of contempt for the independent bird-watcher. Another point concerns the title, which might more accurately be written "The Art of finding Ecology interesting," or "The Art of making Naturalists do Scientific work." But perhaps the title is only meant to suggest that scientific research can indeed be a sport and a pastime. The lucid style, unbiased views about such important subjects as bird systematy, and the well-informed and modern outlook, make the book a powerful aid to ornithology and ecology in this country.

Turning to the future we may ask how field work on British birds will develop. The present trend is for counting birds—a sort of stock-taking of our ornithological possessions. Ten years ago bird courtship was the fashion, and before that bird migration. All these aspects of bird ecology have tended to acquire a welter of raw facts, without clear vision

of their significance. It is partly for this reason that British ornithology can no longer remain unorganised. Migration work (through H. F. Witherby's ringing scheme) has for some time been centralised. The proposal for a national centre at Oxford for the co-ordination of field studies on birds and the assistance of ornithologists has already received powerful support among ornithologists, and Nicholson's book forms a valuable outline of the methods and aims which such an institute might follow.

C. E.

SALMON AND TROUT CONSERVATION.

- (1) **Wye Board of Conservators.** *Annual Report, Season 1931.* Hereford.
- (2) **E. B. Phelps and D. L. Belding.** *A statistical study of the records of salmon fishing on the Restigouche River* (privately printed)¹.
- (3) **E. Percival.** *On the depreciation of trout fishing in the Oreti (or New River), Southland: with remarks on conditions in other parts of New Zealand.* New Zealand Marine Dept. Fisheries Bull. 5, 1-48. Price 1s. 9d. Government Printing Office, Wellington, N.Z. 1932.

(1) The Wye Board of Conservators legally controls the fishing methods over the whole of the waters which drain into the Wye—some 1650 square miles, the length of the main river being about 150 miles. In 1931 about 23 tons of salmon were taken out, and of this over 15 tons was caught by rod and line, the rest being netted in the estuary. It will be seen that the responsibility of administering this (for England) large freshwater fishery, and of ensuring that it is neither under-fished nor over-fished, is no light one. The actual production of salmon, though obviously significant, is less important than the amenities provided by the fishing. Although salmon fishing as a sport may not be agreeable to nor within the means of everyone, there is no doubt that it provides an important safeguard against the pollution or other exploitation of a very fine river. For naturalists and ecologists especially this is a matter of direct interest. The Board has already encouraged a preliminary survey of fish-food resources, which was carried out by W. Rushton ("The fish-food of the Wye," *Salmon and Trout Magazine*, 1931, 1-15).

The control of salmon fishing would be complicated even with a constant salmon population. But salmon are subject to fluctuations in numbers. The Wye Board has been able, by the collection of information and statistics from nearly all their licence holders, and by sample scale-readings, to follow the changes in age distribution of the salmon population from year to year. The report says "it is not the duty of the Board to make forecasts," and then very sensibly proceeds to do so. The basis for these forecasts seems sound. The method adopted is the same in principle as that used by Hodgson (see present number, *J.A.E.* p. 108) for herring, and the results for Wye salmon may be summarised as follows:

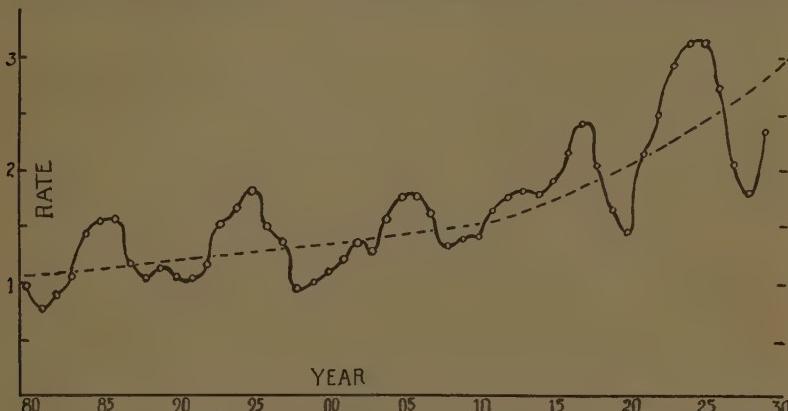
| Years | Year-classes | | | |
|----------------|--------------|------|------|-----|
| | grilse | 4 | 5 | 6 |
| 1927 | ab. | ab. | ab. | ab. |
| 1928 | few | ab. | ab. | ab. |
| 1929 | few | few | ab. | ab. |
| 1930 | more | few | few | ab. |
| 1931 | ab. | more | few | few |
| Forecast: 1932 | ? | ab. | more | few |

An interesting point brought out is that the 1924 spawn grew into young smolts which were very abundant in 1927, but had become greatly reduced by the time they were grilse in 1928. The failure of salmon is therefore to be sought in some environmental factor acting on smolts during their life in the sea or migration in estuaries. The main catch of fishermen is in five and six year old fish, and failure of this catch is due to factors operating several

¹ Read at the Matamek Conference on Biological Cycles (Canada, 1931). To be published later.

years before. This is what enables forecasting to be developed. For complete success it is clear that investigations will have to include marine and estuarine conditions. The impression left after reading this Report is that conservation of the Wye is under sane and intelligent control, which requires further field research along ecological lines to render it fully effective.

(2) The Restigouche Salmon Club, which fishes the Restigouche River in New Brunswick, Canada, is a very exclusive American organisation, which has always had a remarkably strong tradition or rule about recording fish statistics. There are records for each year since 1879 of the date, place and weight of each fish caught by each member. Since 1905 the total fishing-time of each member was also recorded, so that the number of fish per rod per day could be calculated. A method of extending this to the early years was invented (the mathematical computations are throughout very carefully and ingeniously checked, and the report is a fine example of the intelligent use of statistics). The figures for 52 years were plotted. They showed extreme fluctuations. A simple smoothing ($a + b + c = \text{successive three year means}$) eliminated very short periodicities, and the resulting curve shows a remarkable ten-year cycle in numbers, with a major rising trend. This curve is reproduced below.



The three-year moving average rate of fishing (all fish), 1880–1929. Connecting line sketched. Geometric trend lines previous to and following 1910. (Reproduced by permission.)

This Report was read at the Matamek (Canadian) Conference on Biological Cycles in 1931; it was noticed with surprise that this ten-year cycle in New Brunswick salmon ran exactly parallel to the great fur cycle of the Canadian forests—shown most strikingly by the snowshoe rabbit and the lynx. The years of rabbit abundance coincide in general with those of high salmon catch. The salmon statistics are analysed in other ways which can only be briefly referred to here. One feature is the construction of a formula by which both the smoothed curve and the original curve can be closely simulated.

Young salmon spend a variable number of years in the sea. There is no connection in these statistics between the number of breeding fish and their returning offspring. But there is a pronounced connection between the abundance of successive year-classes returning. The authors develop their argument to show that the cycle must be caused by factors of an oceanic or tidal nature, probably acting on the smolts during migration. This conclusion falls into line with the Wye investigation discussed above. It is an important conclusion from the general point of view of conservation, since it brings the whole question of marine fishery fluctuations into relation not only with salmon runs but also with the fluctuations in Canadian forest life which in turn influence strongly the fur trade and the general welfare of people in the northern wilds of Canada.

(3) The settlement of a new country always brings in its train a host of conservation problems, and these have been especially acute in New Zealand, where the passion for introducing European forms of animals and plants has in the past been given full rein. Trout had been put into the Oreti River at intervals from 1870 onwards, and the author chose it as his special area for study both because it was a good example of the general freshwater fishery problem occurring in other parts of the country, and also because of the fishing diaries of MacKay, which cover a long period of years. Percival was faced with the task of examining and sifting the numerous beliefs of fishermen and the theories of naturalists and biologists about the history and alleged recent decline in size of the introduced brown trout (*Salmo trutta*). It may be noted at once that the casual theories of biologists turned out to be as nebulous and as of little value as the beliefs of anglers. Briefly they were these: trout had declined in size during recent decades; this was due to the exhaustion of their natural food supply (aquatic invertebrates), also to the increase in whitebait (*Galaxias*) fishing in the estuaries depriving older trout of an important food item; this food shortage caused slower growth of trout; deforestation, by causing floods which silt the rivers and therefore destroy trout food organisms had also contributed to the shortage; foreign birds had reduced the land insect fauna (e.g. grasshoppers) which might otherwise have fallen into the rivers and been eaten by trout, a situation also brought about by deforestation which removed underbrush on the river banks. But behold the result of the first proper quantitative ecological study of these problems by the author. The invertebrate fauna of rivers is very rich still (thus there were 683 invertebrates to the square foot on one area with a huge fish population not only of trout, but also of eels, smelts, etc.—most of the organisms being caddis larvae and mayfly nymphs which are important trout foods); the whitebait fishery has not affected the trout; trout do not in fact grow any slower than they used to do; the forests have been usually replaced by grassland which is a first-rate safeguard against erosion and flooding, but one river which had become silted heavily as a result of deforestation into waste land around it contained a rich invertebrate fauna living in and on the silt; the grasshoppers began to decrease before introduced birds had become an important factor. But the decrease in average size of trout caught is an undoubted fact. Percival shows that it is probably entirely due to over-fishing which removes too many of the fish, especially larger ones. The practical remedy is a simple one—to allow the trout to grow older before catching them. This can be done by suitable restrictions in fishing. Percival's investigation, which includes a mass of interesting ecological data and is mainly based on quantitative sampling and the intelligent comparison of different waters (using them as natural one-factor experiments), forms a remarkable indictment of slipshod field work and of the opinions and theories of the "practical man." It is also interesting to note the tendency to blame someone else (God, circumstances, or farmers) for conditions which were entirely under the control of anglers themselves. It is a noteworthy step forward to have a competent quantitative study by a trained ecologist, sponsored by the Government. The author's methods were originally worked out on rivers in Yorkshire along what would be called academic ecological lines, and these results were published in the *Journal of Ecology*.

C. E.

THE PHYSIOLOGY OF MIGRATION.

Walter Heape. *Emigration, migration and nomadism.* Edited and with Preface by F. H. A. Marshall. Pp. 1-369. Price 12s. 6d. net. W. Heffer and Son, Cambridge, England, 1931.

WHEN an experienced physiologist undertakes a thesis on an ecological subject the result should be of considerable benefit to ecologists—and physiologists. Heape's posthumous work is a difficult book to review because it contains so much sound reasoning on physiological data but at the same time ignores many basic principles of animal ecology. It is

obviously unfair to review such a work in the light of recent advances in ecology, since the author died in 1929 and his book was written in the dark infancy of animal ecology when he had no chance to incorporate the knowledge which has since been obtained by ecological workers. Dr Marshall has, however, ably edited the work, and by means of concise and appropriate footnotes indicated the lines on which more recent work affects the conceptions of the author.

The main line of argument is that most movements of animals (emigration, migration, etc.) can be traced directly or indirectly to functional disturbances of the reproductive system and the endocrine glands. The two principal premises on which the author's theories and explanations are based are: (1) The existence, among practically all animal species, of definite laws of territorial rights, either for species, colonies, families, or individuals. (2) The presence of a reproductive stimulant or "excitant" (vitamin E) in excessive quantities in vegetation at certain times, or alternatively a great variation in the effects of this stimulant upon animals at different times. This latter idea has received considerable support from the research work on vitamins carried out since the book was written, but proof of Heape's conceptions of its function in controlling reproductive activity in nature has yet to come. The ecologist generally finds that things do not work out so simply as this.

The existence of territory among many birds and carnivorous mammals is now, of course, a proven fact, and many useful and interesting examples are here set forth, but Heape goes further in postulating the observance of strict territorial rights among herbivorous animals, and even suggests that in some instances the carnivores respect the territorial rights of the animals they feed upon. The ecologist will be somewhat startled to find some of his most knotty problems explained away on simple physiological grounds, while more simple occurrences in the lives of animals are invested with surprisingly complex motives: the termination of periodic increases among rodents is explained as being due to exhaustion of their reproductive capacity, while the complicated ecological factors such as the effects of epidemic disease, resulting minimum density of numbers, and the influence of population density on the rate of increase are barely considered. And surely the seals that bask on the seashore, surrounded by penguins, simply want to rest and digest the penguins they have caught and eaten while in the sea; the fact that they do not then molest the penguins need not imply a recognition of the penguin's territorial rights to the shore—and anyway the seal is obviously built for catching his food while in the water, not on land. There does not seem to be much evidence in fact that territorial rights are observed among more than a few particular species. It is rather difficult to distinguish between competitive dominance of a species and territorial rights. Food preferences and environmental conditions may also give rise to the impression of territory holding, whereas in reality other species may not want to eat that particular food nor live in that particular environment. A thorough knowledge of the habitats and optimum environmental conditions for each species concerned is essential before one can talk with assurance about territories.

The three chapters on emigration, as distinguished from migration, are extremely interesting and bring together a vast amount of data published in scattered journals and books, and, although in some cases the ecologist will fail to agree with the author's explanations of the causes and factors controlling emigration, he will find much to stimulate thought and argument here as in every other part of the book—and this is admittedly the author's main purpose in writing it. A valuable and extensive bibliography is appended.

One cannot help lamenting the fact that this important work should have been written without the author having any opportunity of absorbing the knowledge which is now accruing from the scientific study of animal ecology and animal numbers in particular. The viewpoint is naturally physiological, and it is unavoidable that in many cases physiological explanations are insufficient where psychological and complex ecological factors are working concurrently, as they must do in such matters as emigration, migration, and fluctuation in numbers.

A NOCTURNAL COMMUNITY.

Orlando Park, John A. Lockett and Dwight J. Myers. *Studies in nocturnal ecology with special reference to climax forest.* Ecology, 12, 709-27, 1931.

THE observations made by the writers in beech-maple forests in north-east Ohio are, like most ecological field studies, incomplete. But they are full of interest. They form the first systematic attempt to study the active nocturnal component of any animal community. Transects were made through the woods, with a number of stations chosen in representative minor habitats, and the active animals observed and counted and identified. By carrying on for some twenty-four hours adequate comparisons with diurnal conditions were obtained. Twenty-five species of animals were found to come out at night and to show a marked rhythm of activity (they included nineteen species of beetles—carnivores such as carabids, staphylinids, and a tiger beetle, also fungus eaters and others—a millipede, two snails, a frog, a salamander, and a newt). One species of ant (*Aphaenogaster fulva*) was active both by day and by night. It is made clear that special attention was paid to these groups, which do not form the whole of the nocturnal fauna. The behaviour of these forms is interesting, and in many instances the food habits were ascertained. It would have simplified the reading of the paper if the feeding habits had been listed with the species instead of scattered in the text. Mention is made of diurnal forms found at rest during the night: it would be of great interest to know how far these are preyed upon by nocturnal predators, and how far the community is self-contained. Readings of temperature, relative humidity, and evaporation rate were taken at certain stations, and correlated with the activity of the more abundant forms. Three of these (the two snails and a fungus-beetle) were definitely more active as the temperature fell and the relative humidity rose, and these results fitted in with the less complete data obtained for other forms. The writers point out that these findings require extensive further analysis in the laboratory, and also that some of the animals may have inherent physiological rhythms. The paper ends with a discussion of the nature of such rhythms and their relation to the environment. The whole investigation appears to have been carried out with admirable care and it opens up a wide vista of field and experimental study.

C. E.

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by
CHARLES ELTON
(EDITOR)
and
A. D. MIDDLETON
(ASSISTANT EDITOR)



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